HERTER, DALE REUBEN

HABITAT USE AND HARASSMENT OF SANDHILL CRANES STAGING ON THE EASTERN COPPER RIVER DELTA, ALASKA

UNIVERSITY OF ALASKA M.S. 1982

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HABITAT USE AND HARASSMENT OF SANDHILL CRANES STAGING ON THE EASTERN COPPER RIVER DELTA, ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfullment of the Requirements

for the Degree of

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By

Dale Reuben Herter, B. S.

Fairbanks, Alaska

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HABITAT USE AND HARASSMENT OF SANDHILL CRANES STAGING ON THE EASTERN COPPER RIVER DELTA, ALASKA

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ABSTRACT

Migration and staging activities of lesser sandhill cranes (*Grus canadensis canadensis*) were studied in spring 1979 and 1980, and fall 1979, 1980, and 1981 on the eastern Copper River Delta, Alaska. Migration peaked in late April and early May, and from mid- to late September. All resightings of 43 lesser sandhill cranes color-marked during winter 1980 in California have come from Pacific Flyway states, including 6 resightings on the Copper River Delta. Age ratio observations of crane flocks indicated 7% juveniles in fall 1979 and 1980, and 11% in 1981. Staging cranes fed almost exclusively on the bulbs of arrow-grass (*Triglochin palustris*) in habitats dominated by *Carex ramenskii* and several moss substrates. Aircraft caused greater disturbance of cranes than did humans or eagles, but planes remaining 150 m or higher over feeding crane flocks should result in minor disruption of staging cranes.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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INTRODUCTION

Sandhill cranes (*Grus canadensis*) are one of the most far-ranging breeding birds in North America. During the nesting period, they are distributed from Cuba and the continental United States to northern Canada, Alaska, and northeastern Siberia (Walkinshaw 1949). The northernmost subspecies, the lesser sandhill crane (*G. c. canadensis*), annually migrates from its arctic and subarctic nesting areas to wintering grounds in the southwestern United States, from central California to Texas, and Mexico. Although they nest in isolated pairs, cranes become gregarious during fall migration and remain in large flocks until arrival on breeding areas the following spring. Most populations of sandhill cranes utilize traditional stopover sites, known as staging areas, along migration routes to rest, feed, and gather in preparation for continued migration (Walkinshaw 1960, Madsen 1967, Krapu 1979).

The Copper River Delta (CRD), located along the south coast of Alaska, provides important wetland habitat for over 20 million migrating waterfowl and shorebirds (Islieb and Kessel 1973, Islieb 1979, Mickelson et al. 1980) (Fig. 1). It also provides critical nesting habitat for trumpeter swans (*Olor buccinator*), dusky Canada geese (*Branta canadensis occidentalis*), Aleutian terns (*Sterna aleutica*), and other waterbirds (Hansen et al. 1971, King and Lensink 1971, Bromley 1976, Holtan 1980). For migrating birds utilizing

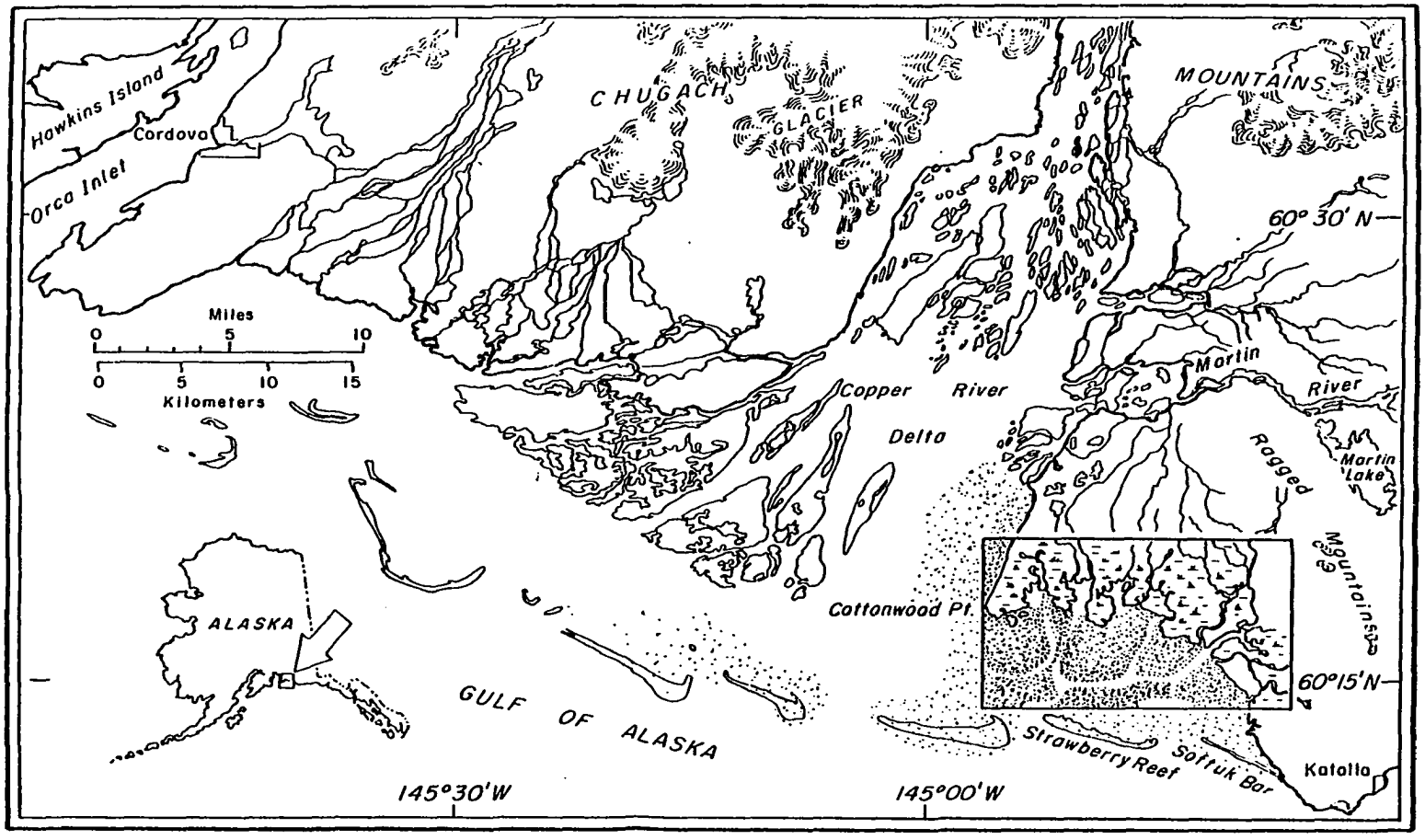

Figure 1. Location of the eastern Copper River Delta study area (rectangle).

Pacific Flyway routes, the CRD is the largest region along the steep and rocky northeastern Pacific coast that offers extensive marshes and tidelands for staging activities. Sandhill cranes were first identified in the literature as common migrants on the Copper River Delta by Islieb and Kessel (1973). Local residents have long noted use of the eastern portion of the Copper River Delta by staging sandhill cranes, particularly during fall migration (R. Gill, M.E. Islieb pers. comm.). My study examined the importance of the eastern Copper River Delta (ECRD) to sandhill cranes.

Recent studies of sandhill cranes on other staging areas have emphasized the physiological and social importance of these sites to migrating cranes (Krapu 1981, Lovvorn and Kirkpatrick 1981). The birds utilize staging areas to rest, feed, and put on additional fat deposits, to conduct courtship displays in spring to renew or maintain pair bonds, and to strengthen family-group associations. Because cranes are generally fair-weather migrants, staging may also occur when foul weather hinders further movement (Alerstam and Bauer 1973). Even though birds may remain on staging grounds for only a few days or weeks, the strategic location, food availability, and lack of disturbance on such areas may render these areas essential over the annual cycle of migrant sandhill cranes.

Timely information on the importance of coastal wetlands along the Gulf of Alaska to wildlife is essential for several reasons. Planned development of petroleum, mineral, and timber resources in

this area could impact wildlife directly, by pollution of the surrounding environment and habitat destruction, or indirectly, through increased human population and disturbance levels. Baseline data on habitat needs (both spatially and temporally), and tolerance levels to human activities are required to identify critical use areas and to mitigate potentially detrimental disturbance of wildlife. The proximity of the ECRD to oil, coal, and timber reserves makes this area particularly vulnerable to potential development conflicts. Low level aircraft flights associated with a local salmon fishery and resource inventories, and recreational use of ORV's, airboats, and planes have been increasing on the CRD. Management techniques to handle increased human presence in this relatively pristine area are needed. Plant communities on portions of the CRD important to waterbirds are currently undergoing rapid successional changes as a result of uplift from the 1964 Alaska Earthquake (Shepherd 1965). Changing use patterns by birds should be monitored to enable accurate assessment of future habitat availability.

The initial objectives of my study were to:

1. describe the migration pattern of sandhill cranes through the ECRD, including abundance, timing, and duration of staging by cranes;
2. investigate food preferences of staging cranes;
3. determine characteristics of feeding and roosting sites, as well as overall habitat use by staging cranes;

4. determine recruitment levels of this population by counts of juveniles;
5. assess the affects of human-related disturbance on cranes, specifically aircraft harassment.

Due to later assessment of data and opportunity to conduct banding of cranes, information on: 1. measurements of cranes and discussion of subspecies affiliation, and; 2. migration pathways, wintering grounds, and probable breeding areas of ECRD cranes is presented.

Status of all bird and mammal species observed on the ECRD is presented in Appendices I and II. Species designations follow the American Ornithologists' Union and supplements (1957, 1973, 1976) for birds, Jones et al. (1975) for mammals, and Hultén (1968) and Crum et al. (1973) for plants.

Observations of cranes were achieved concurrently with research on all birds on the ECRD from 27 April-22 October 1979. Specific investigations of cranes were conducted from 19 April-20 May and 18 August-20 October 1980, and 27 August-28 September 1981. Banding operations were carried out at Merced National Wildlife Refuge, California, from 28 December 1971-11 February 1980.

STUDY AREA

The Copper River Delta forms an expanse of over 650 km^2 of level marshy terrain along the otherwise mountainous southcentral Alaska coast. The eastern Copper River Delta covers over 200 km^2 and lies between 60°10' and 60°25'N. latitude and 144°30' and 145°00' W. longitude (Fig. 1). For this report, the ECRD is considered that area of supratidal marsh, saltmarsh, and intertidal mudflats bounded on the east by the Ragged Mountains, the north by the Martin River, the west by the Copper River, and the south by the Gulf of Alaska.

The ECRD forms an "island" of open marsh habitats within the western hemlock (*Tsuga heterophylla*)-Sitka spruce (*Picea sitchensis*) coastal rainforest ecoregion. Rugged mountains, glaciers, and dense coastal forests dominate the area. Close proximity to the Pacific Ocean results in a maritime climate of cool summers and mild winters with abundant precipitation during all seasons, but particularly in fall (Table 1) (Islieb and Kessel 1973, Selkregg 1974). Prevailing wind direction is southeasterly or easterly, and winds of gale force (50-100 km/h) or greater occur regularly from September to June.

A series of barrier islands and bars extends along the seaward margin of the study area. The sandy outer beaches absorb the predominantly southerly oceanic swell, while the inner beaches form portions of the intertidal mudflats and saltmarsh. The barrier

Table 1. Mean weather statistics (1970-1979) for the Copper River Delta, taken at the Cordova Federal Aviation Administration (FAA) weather station.

Month	Temperature(°C)	Precipitation(mm) (includes snow)
January	-5.0	156.0
February	-2.9	163.1
March	-1.6	149.6
April	2.2	145.0
May	6.5	152.3
June	10.2	118.8
July	11.9	179.8
August	11.7	227.2
September	8.9	292.9
October	4.2	313.4
November	-0.8	212.7
December	-4.1	189.2
Total		2300.0

islands and bars visible from ECRD camp sites included Softuk Bar in the far southeastern corner of the CRD, Strawberry Reef, and an unnamed island immediately to the west (Figure 2). Sand dunes dominate the central ridges of barrier islands and bars. Older dunes are covered with beach rye-grass (*Elymus arenarius*) and some alder (*Alnus sinuata*), willow (*Salix* spp.), and Sitka spruce scrub.

Behind the barrier islands is a tidal estuary, locally known as Softuk Lagoon. Its waters cover all mudflats during very high tides. Tidal currents up to 2 m/sec flow through the inlets between islands, which are concentration points for migrating salmon (*Onchorhynchos* spp.) and salmon gillnetters. Tidal range measured at Cordova, approximately 64 km west of the study area, is 6.5 m during highest spring tides and averages 3.5 m (U.S. Coast and Geodetic Survey, Tide Tables). High tides inundate variable portions of the mudflats twice daily. Intertidal mudflats are interrupted only by deep tide channels draining the supratidal marsh.

A narrow band of saltmarsh (0-2 km wide) is present immediately landward of the tidal lagoon and mudflats (Fig. 2). Freshwater marshes occur over the remainder of the ECRD, excluding isolated uplands of coniferous forest (the Spruce Islands) and river dunes covered with alders and cottonwoods (*Populus trichocarpa*). Relatively open freshwater marsh with patches of shrubby growth are found on the central study area above the saltmarsh and extend to the limit of tidal influence. Large tidal sloughs navigable with small boats

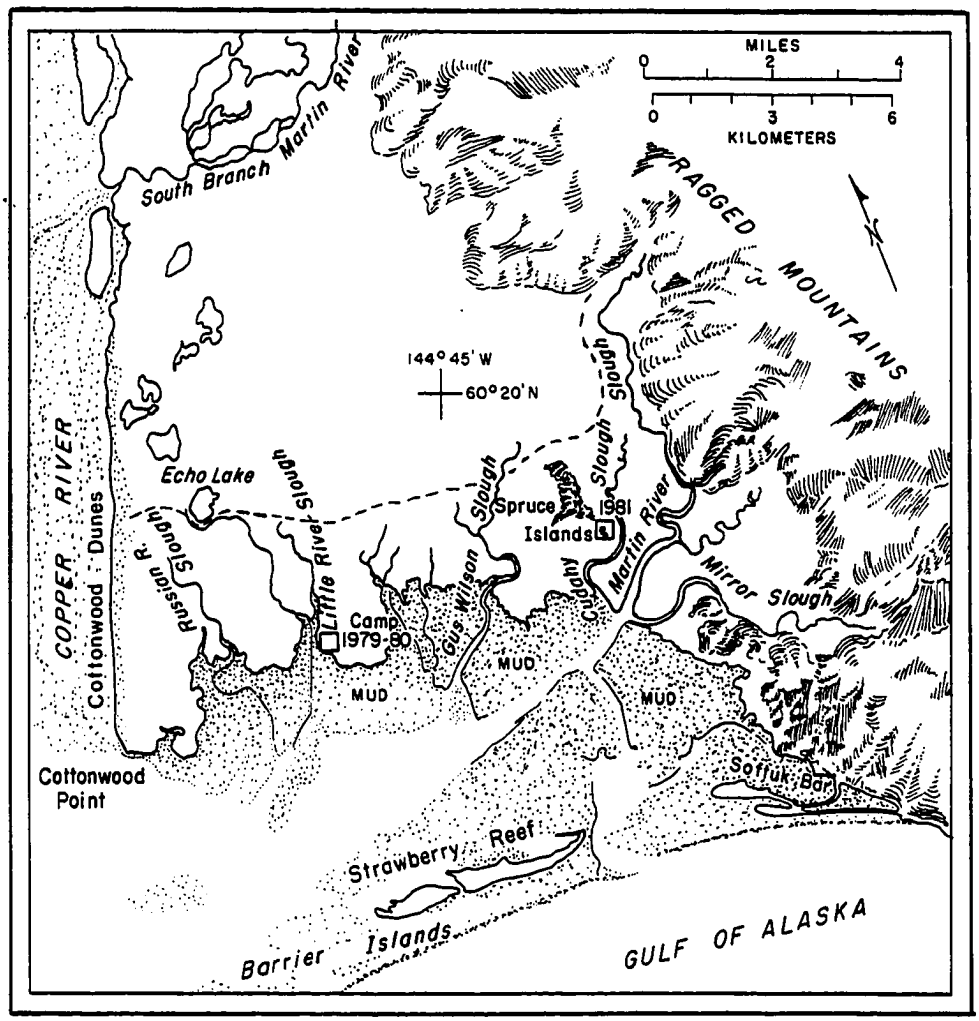

Figure 2. Place names and camp locations on the eastern Copper River Delta, Alaska, (dashed line indicates extent of tidal influence within slough channels).

at or near high tide, drain this area in a general north-south direction. Cudahy Slough and, to a lesser extent, Gus Wilson Slough, were used as floatplane landing sites servicing the local commercial fishing fleet. Lower Cudahy Slough was used as an anchorage for up to 50 fishing vessels at a time, usually between regulated fishing periods and during stormy weather. Occasional small shallow ponds with gently sloping margins and a network of small sloughs also provide limited open water habitat in this area.

Shrub-dominated freshwater marshes occur above the limits of tidal influence and extend to the Ragged Mountain and Martin River borders. Large lakes, streams, and beaver ponds occur throughout this area, (see Section V for further descriptions of habitat types). Plant ecology of the entire CRD has been discussed by Crow (1968).

The geomorphology and geologic history of the Copper River Delta has been reviewed by Reimnitz (1966) and Galloway (1976). A combination of fluvial, marine, tectonic, and surficial processes have contributed toward the uniqueness of ECRD wetland habitats. Reimnitz (1966) estimated that the Copper River transports 107 X 10^6 metric tons of sediment a year, or 1/4 as much as the Mississippi River. Westerly flow of longshore ocean currents carries the majority of sediment westward from the mouth of the Copper River, with deposition as far west as Cordova. Fine particulates tend to filter eastward, forming mudflats on the ECRD, while sandflats form

over much of the western Copper River Delta (WCRD) (Galloway 1976). Westerly ocean currents also bring highly saline tidal water into the ECRD, whereas freshwater outflow from the Copper River produces less saline water in tidal lagoons on the WCRD.

The northern Gulf of Alaska coast is one of the most active seismic regions in the world. The 1964 Alaska Earthquake (8.3-8.6 on the Richter Scale) uplifted the CRD 1.8-3 m, with highest uplift on the eastern and far western portions of the delta (Remnitz 1972). This resulted in large areas of saltmarsh formerly inundated by high tides to become supratidal freshwater marsh. The heavy rainfall of the region flushed salt deposits out of sediments lifted above tidal influence and permitted growth of salt-intolerant plants, including a dense ground cover of mosses, and allowed invasion of woody shrubs over former open saltmarsh. New saltmarsh is forming on the ECRD over areas that had been barren mudflats.

METHODS

I. MIGRATION AND STAGING

To determine phenology and abundance of migrating and staging sandhill cranes, I conducted watches of 1 h duration every 2 h during all migration periods. Watches varied greatly, however, during periods of peak migration when watches were often continuous for 4-5 h, or during times of low activity or bad weather when occasionally no watches were conducted for 24 h or more. Table 2 summarizes total observation hours during all field seasons on the ECRD study area. I conducted migration watches from a 4-m high wooden tower located at the field camp during 1979 and 1980, and from 2 wooden platforms placed 10-15 m high in Sitka spruce trees on each of the two Spruce Islands (Fig. 2). I used 8-10x binoculars and 15-60x zoom spotting scopes to locate and follow crane flocks. Movements of cranes were recorded in field notebooks and on maps of the study area. I recorded observations of crane behavior opportunistically during migration watches or from the ground during other investigative activities. A general weather synopsis for the local area was recorded at the end of each day. Specific hourly weather information was later obtained from the Cordova FAA weather station located on the western Copper River Delta, approximately 40 km west of the ECRD. Data on precipitation, wind speed and direction,

Table 2. Migration watch periods and total observation hours on the ECRD study area.

	Migration watch period	Total hours of observation
1979		
Spring	27 April - 30 May	(est.)100.00
Fall	20 August - 22 October	231.50
1980		
Spring	17 April - 19 May	213.00
Fall	17 August - 15 October	223.25
1981		
Fall	27 August - 28 September	204.00

temperature, cloud cover, and cloud ceiling height were obtained from this station.

II. MIGRATION ROUTES

In an effort to determine breeding and wintering areas and migration routes of the sandhill crane population staging on the ECRD, I attempted to capture and color-mark cranes on the study area. Three taxidermy-mount decoys were placed near the field camp and sets of 18-kg test monofilament snares were set near the decoys. From 50 to 75 monofilament loops were attached to a central line, staked at both ends, and hidden in surrounding sedge cover. In addition, cranes roosting on mudflats near the field camp were approached on cloudy nights from 20:30 to 22:30 ADT with a strong light and a long-handled net. While one worker held the light and walked toward a crane flock, the other remained behind the light beam with the net until a crane was approached close enough for capture.

Like most other migratory waterbirds on the ECRD, sandhill cranes were thought to use a Pacific Flyway migration route. From 28 December 1979 to 11 February 1980, I attempted to capture and color-mark wintering lesser sandhill cranes at Merced National Wildlife Refuge (NWR), California, in hopes of resighting marked

birds on the ECRD. Following the suggestions of Wheeler and Lewis (1972) and Ramakka (1979), 2 to 4 recoilless rocket nets 20 m X 10 m and 30 m X 15 m were placed in a harvested corn field and camouflaged with surrounding plant debris. Two nets were placed facing each other at each set, with 6 taxidermy-mount crane decoys and ear and shelled corn placed near the nets to attract feeding crane flocks to the trap site. All nets contained a 1-m wide skirt around the periphery to prevent escape once cranes were netted. Rocket angles were set at 45° and extra propellent included in the rockets to carry the net over and beyond the relatively tall birds. Captured cranes were marked with standard aluminum leg bands and red plastic neck collars and leg bands. Both color-markers were 62.5 mm high and contained matching white alpha-numeric codes.

Whenever possible, I inspected cranes on the ECRD for neck collars, using binoculars and spotting scopes during age ratio counts in 1980 and 1981. Letters and flyers were sent out to inform government personnel associated with land management agencies and other observers of the banding program. A thorough search of the literature and canvassing of observers along the probable migration pathway to describe crane passage in their areas was conducted to better delineate migration routes.

III. SUBSPECIES IDENTIFICATION

To determine the subspecific identity of cranes on the ECRD, I took standard ornithological measurements on most cranes bagged by hunters and cranes collected for food habits analysis. Cranes were measured to the nearest millimeter as to length of exposed culmen, bill length from the posterior edge of the nares to the tip, wing chord (not flattened), tarsus, middle toe, and total body length. In addition, weights of whole crane carcasses were taken whenever possible.

Measurements of crane tracks were taken opportunistically. Each well-defined track on a linear transect across use areas was measured from the back of the "heel" to the end of the middle toe excluding the claw. I only measured tracks at approximately 1 m intervals along each transect to avoid measuring the same bird's tracks more than once. To exclude the possible bias of smaller tracks of juveniles, only spring measurements were included in the analyses. With the use of BMDP Biomedical computer programs (Dixon and Brown 1979), a chi-square test for normality was conducted, as were tests for skewness and kurtosis of the track frequency distribution.

IV. FOOD HABITS

To determine food selection preferences of staging sandhill cranes, I collected 15 cranes and obtained the remainder of food samples from hunter-killed birds. Cranes were collected with the use of a .222 rifle with a 2-7x mounted zoom scope in spring and a 12-gauge shotgun in the fall. Cranes were usually collected opportunistically, but whenever possible, birds were observed feeding for 30 to 60 min before collection to ensure a full gullet, as suggested by Reinecke and Krapu (1979). Due to lower use of the ECRD in the spring by staging cranes, I collected food samples from only 2 birds in spring 1979 and 1 in spring 1980. High hunter success and prolonged staging by cranes in the fall of 1979 allowed collection of 12 cranes by field personnel and 67 food samples from birds bagged by hunters. I did not concentrate on obtaining extensive food habits data in fall 1980 or 1981 due to the already large sample size obtained in 1979 and the predominance of one food item in the diet of staging cranes. Seven food samples were obtained in fall 1980 and 1 in 1981. Incidental observations of feeding birds and interviews with local hunters also revealed information on food preferences.

The gizzard and gullet (esophagus and proventriculus) of all specimens were removed as soon as possible after collection. The contents were separated and placed in 10% formalin in the field. Upon return to the University, samples were drained of formalin and

frozen for later examination. Food items from gullets were separated by taxa and measured volumetrically, then oven-dried at 60° C for 48 h and weighed. Contents of gizzards were measured volumetrically, then shaken with water in a graduated cylinder to separate and measure the grit fraction. Ocular estimates of volumes were then made on the remaining food material in a broad sorting pan with the aid of a 10x dissection scope.

I expressed frequency of occurrence of food items in the diet of cranes as the percent of all gizzards or gullets containing a given food. Percent by volume was determined using both the aggregate-volume and aggregate-percentage methods described in Martin et al. (1946) and Swanson et al. (1974). Percentage by dry weight of a food item over total dry weight of all foods was also calculated for gullet contents. I used this variety of food habits analyses to ensure comparability with other food habits studies of sandhill cranes (Guthery 1975, Lewis 1979*b*, Mullins and Bizeau 1978, Reinecke and Krapu 1979), where one or several of these different methods were used.

In late fall of 1979, I collected 1100 *Triglochin palustris* bulbs from a 6-m^2 area of wet meadow habitat and air-dried them in the field. The samples were subsequently oven-dried at 60° C for 48 h and sent to the University of Alaska Plant and Soils Laboratory in Palmer, Alaska, for nutritional analysis.

V. HABITAT USE

All local flights of staging crane flocks I observed from the tower at the field camp in 1979 and 1980 were recorded on maps of the study area. I summarized relative use of different portions of the ECRD by calculating total numbers of cranes landing within each survey section (2.56 km^2) of the study area. Due to heavy shrub cover, cranes were only rarely seen on the ground from the observation tower, so relative use of areas based on time spent there by cranes could not be calculated.

I obtained information on plant species abundance within the Wet Meadow habitat by estimating percent plant cover by species on 129 1 m X 1 m vegetation plots. Plots were selected at 200-m intervals along 6 north-south transects 1.31 km apart, covering a major portion of the Wet Meadow. Random starting points were chosen on each transect and all plots were sampled between 19 July and 12 August 1979, a time period corresponding with maximum annual foliage growth for most plant species. Similar 1-m^2 vegetation plots were selected at sites where cranes were observed feeding during September 1980. I opportunistically selected 34 plots at feeding sites during daylight hours as cranes fed. Locations of feeding sites where vegetation plots were sampled in 1980, and systematic vegetation plot transects covered in 1979 are presented in Fig. 3. Feeding sites were also assessed for ground cover type (i.e., mud, water, or

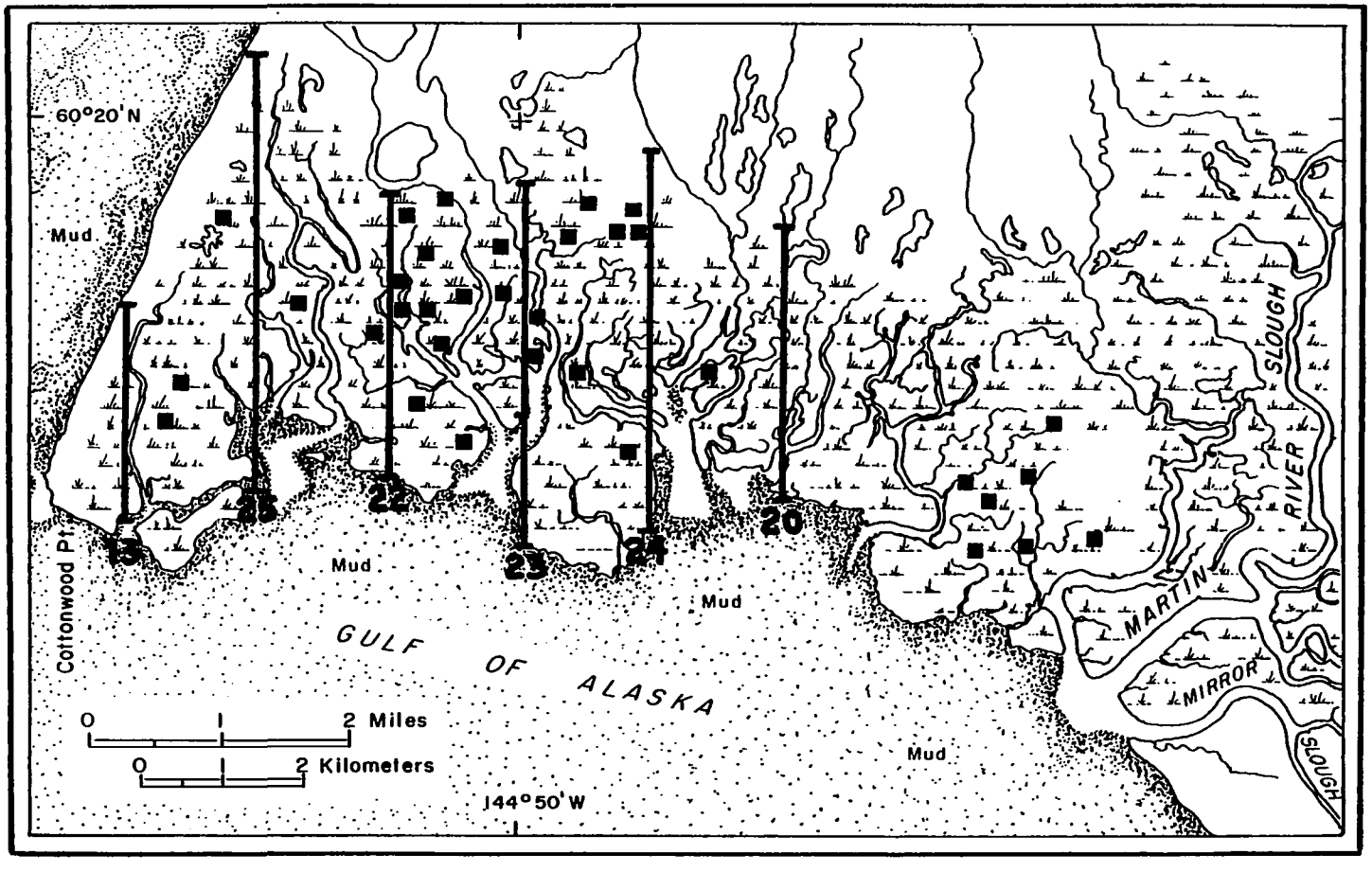

Figure 3. Map of systematic vegetation plot transects with number of plots given for each transect. Squares indicate locations of vegetation plots taken at sandhill crane feeding sites.

moss), surrounding shrub density, size of opening, and moisture regime, as well as percent cover of plants by species, within the plots. BMDP Biomedical Computer Programs were used to conduct principal components analysis of vegetation plots.

Percent cover by species in each plot was used to generate principal components among the 129 systematic vegetation plots. Calculations of loadings of variables on the first 3 components were duplicated for the 34 plots taken at feeding sites. Positions of these plots along the axes of all three components were plotted to define feeding habitat selection based on vegetation patterns. See Davis (1973) and Cooley and Lohnes (1971) for a complete explanation of principal components technique. A Kolmogorov-Smirnov goodness of fit test (Zar 1974) was applied to percent cover frequencies for each species on both plot types to identify plant species most indicative of feeding sites.

To assess availability of feeding habitat to cranes, 16 transects totalling 58.6 km were walked in a north-south direction across Wet Meadow habitat. Transects were spaced 655 m apart. Distance across good feeding habitat along the transects was measured by pacing. I subjectively determined favorable feeding habitat after preliminary analysis of information recorded at feeding sites in September 1980.

By observing crane flocks flying to roost sites from the observation tower and platforms, I identified major habitats used by roosting cranes. Weather and tidal stage data were categorized and

relationships to roost habitat selection were tested with chi-square contingency tests (Johnson 1976). Times of arrivals and departures from roost sites were noted whenever observed.

VI. AGE AND SEX RATIOS

To estimate recruitment levels of young cranes into the population utilizing the ECRD study area, I conducted age ratio counts during the fall observation periods of all three years. The most reliable method of determining juvenile sandhill cranes from adults in the field is by characteristics of the head region (Lewis 1979*a*). The face and forehead, which are fully feathered in juvenile cranes, are gray in color while the crown, occiput, and nape are often tawny. Adult cranes possess an area of bare skin on the crown, forehead, and loral regions that is sparsely covered with short hair-like bristles and is red in color. The nape is feathered and is usually gray. The buffy tips of the wing coverts create a distinct horizontal pattern on most juveniles, and the bill is also usually lighter in color and was found to be helpful in age determination. Following the suggestions of Lewis (1979*a*), age ratios were tallied for those cranes whose heads were clearly discernable as juveniles or adults. Feeding or resting crane flocks were observed at maximum ranges of 100 m using binoculars (7-10x) or 400 m while using a spotting scope (15-60x zoom). Flying flocks were tallied when possible using

binoculars, but rarely were light conditions adequate to get reliable counts. Most age ratio counts were gathered from flocks on the ground, especially those attracted to 3 taxidermy-mount crane decoys placed in an open Salt Grass meadow 300 m from the observation tower in 1979 and 1980. Feeding crane flocks were tallied for percent juveniles from tree-top observation platforms in 1981. I tallied cranes individually across the flock until all were counted or the flock departed. As found by Lewis (1974), adult cranes were usually more alert and raised their heads more often than juveniles. To ensure all juveniles were counted, I waited for each bird to raise its head before continuing counts, unless age could be determined while its head was down.

Age ratio counts were pooled over the entire fall staging period and an overall percentage of juveniles calculated for each year. Subsequently, the fall staging period was divided into 3 equal 15-day periods to detect changes in age ratios throughout the fall. Age and sex ratios of cranes bagged by hunters were also noted. In all cases, sex of cranes was determined by gonadal examination.

Counts of family sizes were attempted on flocks of cranes where age ratios had already been determined. Families could only be discerned when they broke away from the main flock and fed or rested separately.

VII. HARASSMENT

While conducting migration watches from observation points at the field camps, I recorded flocks of cranes flushing from feeding or loafing sites in the Wet Meadow and Salt Grass Meadow. In all cases where a known disturbance source caused a flock to flush, data were collected on: 1. distance to the cranes at flushing (estimated in m), 2. flight direction of cranes in relation to the disturbance source (0-180°), 3. distance cranes flew after disturbance (estimated in m), and 4. time spent in the air (<5, 5-10, 10-15, >15 min). Notes on flock size and amount of time cranes had been at a site before they were disturbed were also recorded. Rarely were all parameters measured or estimated for all disturbances due to frequent inability of the observer to record a disturbance from the onset, varying distances of flocks from observation posts, and preoccupation with other observations. Times and distances were usually estimated and were subject to some observer biases.

Reactions of cranes to humans were most often observed when I approached crane flocks at feeding sites to record habitat use and assess vegetation cover. Distances to crane flocks when they flushed were measured by pacing. Disturbance from hunting was noted whenever possible while hunters were present on the study area, and during collection of birds for food habits data. Notes on crane reactions to bald eagles (*Haliaeetus leucocephalus*) and aircraft

were taken as opportunity permitted. Observations were pooled over all years to provide adequate sample sizes.

To further assess reactions to aircraft, experimental overflights were conducted over staging crane flocks in fall 1980 and 1981. Small float-equipped airplanes (Cessna 185, Beaver) were flown along prearranged flight paths across the study area at altitudes varying from 30-150 m. Reactions of cranes were noted by one observer in the plane and one at an observation platform at the field camp in 1980 or on the Spruce Islands in 1981. The ground observer recorded the previously described disturbance parameters as cranes flushed, while the airborne observer attempted to estimate horizontal distance of the plane to crane flocks at the time they flushed, and response levels to the overflight. Response categories, modeled after Klein (1974) and Davis and Wiseley (1974) included:

1. no response; cranes continued feeding, preening, or resting.
2. alert; a majority of birds in the flock raised their heads and looked at the plane.
3. mild escape; cranes walked or flushed as the plane passed but quickly landed and resumed feeding a short distance away.
4. strong escape; all birds flushed and flew rapidly away from the plane and did not circle and reland at the same site.

5. panic; birds stumbling, running, or flying into each other, disorderly flight away from the plane in all directions, and breakup of the flock.

Reactions to harassment as observed from ground locations were pooled over all 3 fall periods and analyzed by 7 disturbance sources: 1. eagle overflights, 2. eagles pursuing cranes, 3. people approaching cranes while in full view, 4. people utilizing shrub cover and slough channels to approach cranes closely, 5. people hunting (with at least one shotgun fire), 6. small airplane overflights, and 7. helicopter overflights. Additional airborne observations of crane behavior were analyzed separately to further determine response of cranes to aircraft.

RESULTS AND DISCUSSION

I. MIGRATION AND STAGING

A. Timing and Abundance

Sandhill cranes first appeared on the ECRD on 22 April 1979 (flock of 62, J.S. Hawkings pers. comm.) and on 19 April 1980 (flock of 31). Islieb and Kessel (1973) noted an even earlier flock of 27 on 17 April 1969. Numbers of migrating cranes increased rapidly and reached peak numbers during the last week of April and the first week of May (Fig. 4). By the middle of May, most flocks had passed through the area with only a few stragglers lingering through late May (latest, 45 on 24 May 1979). Sandhill cranes used the ECRD only as a stopover point, if at all, during spring migration. Numbers of staging cranes are indicated by the dashed line in Fig. 4 and usually represent birds that had arrived on the ECRD during late afternoon, roosted for the night, then departed west again after feeding and preening for 3-4 h after sunrise. Total crane use-days (number of birds staging multiplied by the number of days present) were also proportionately lower than fall figures (Table 3). On frequent occasions up to 500 cranes roosted overnight, with most leaving the following morning or possibly a day later if

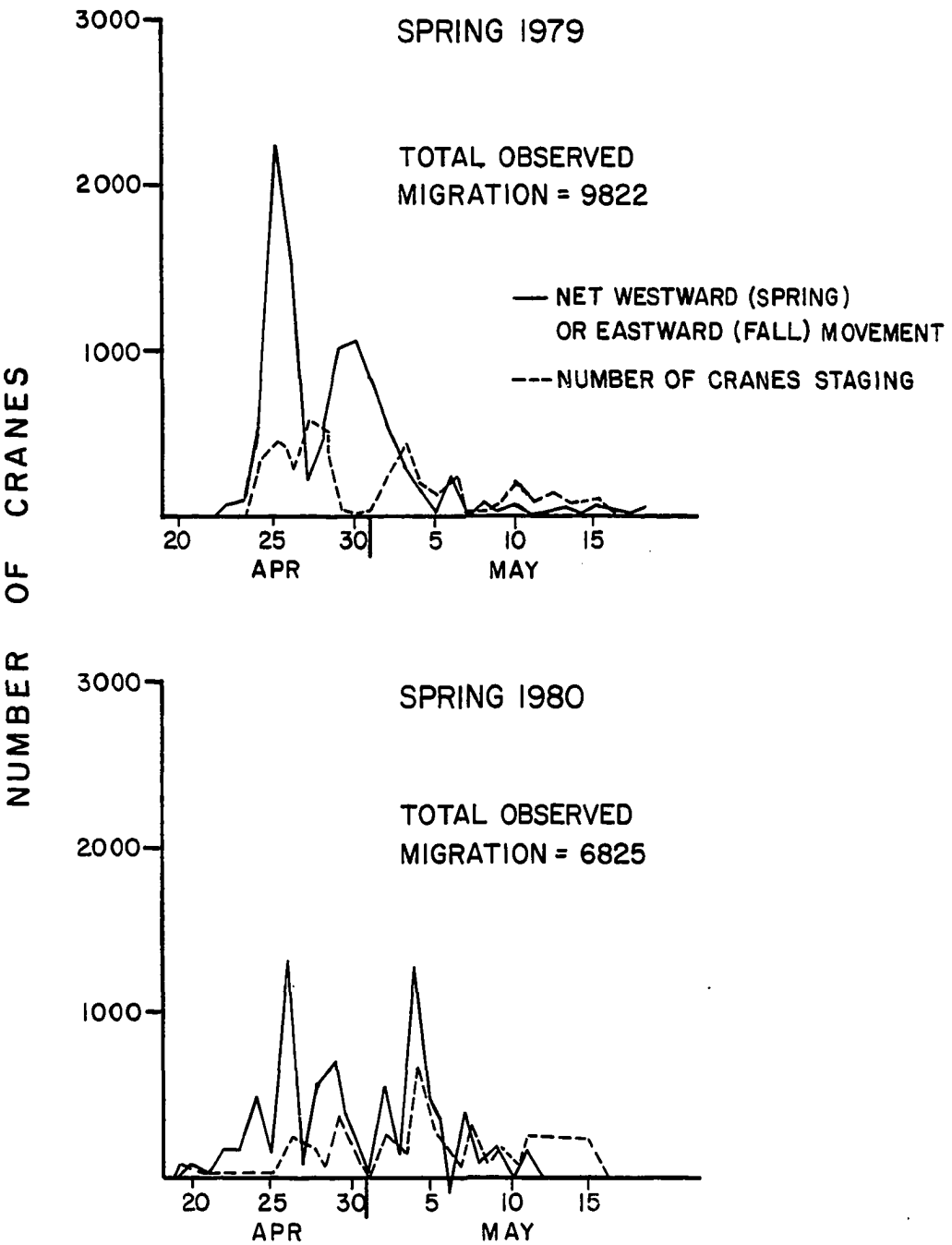

Figure 4. Timing of spring migration and staging activity as observed from the 1979-1980 camp site, eastern Copper River Delta.

Table 3. Total observed migration of sandhill cranes and total crane use-days on the ECRD study area.

Migration period	Number of cranes moving west (spring), east (fall)	Total crane use-days
1979		
Spring	9822	3971
Fall	16,095	41,529
1980		
Spring	6825	4039
Fall	18,038	17,086
1981		
Fall	13,534	19,911

weather conditions were poor after arrival. The majority of flocks observed during the spring however, merely passed by overhead and did not stop, though they often circled over the marsh. During the second week of May in both 1979 and 1980, 95-220 cranes staged on the ECRD for 7-10 days. A female collected from this group on 11 May 1980 for food habits analysis contained undeveloped ovaries, suggesting these lingering birds were non-breeders. Boise (1977) and Drewein (1977) also suggest non-breeding cranes have a more leisurely spring migration based on later arrival dates on the breeding grounds.

As shown in Table 3, roughly half as many cranes were counted passing the field camp during spring migration watches than in fall. By taking into account time spent away from the observation tower during spring migration, estimated passage still only amounts to approximately 12,000 cranes in spring 1979 and approximately 9000 cranes in spring 1980. The lower number of birds counted in spring may be due to several reasons: 1. mortality during fall migration and in winter, 2. wider migration pathways over the ECRD, 3. higher incidence of night migrations, or 4. higher flight altitudes in spring. Mortality to cranes may at times be substantial in fall and winter, mainly from hunting (Lewis et al. 1977), storms (Merrill 1961), collision with power lines (Tacha et al. 1979), and potentially, diseases (Lewis 1974). Mortality alone, however, cannot explain the 50% decline in numbers of cranes counted on the ECRD between fall

and spring. Cranes were noted to fly over a broader area in spring than in fall. Numerous flocks flew over the outer beaches of the barrier islands and over Echo Lake in spring, distances of 5 km or more from the observation tower. Three flocks on 28 April and flocks on 30 April and 1 May 1979 were heard passing west over the barrier islands but could not be located and counted. This, coupled with the reluctance of most flocks to stage in spring on the ECRD, may have contributed substantially to the observation of fewer cranes. While largely diurnal migrants, sandhill cranes are also known to migrate at night (Walkinshaw 1949, Lewis 1974). In interior Alaska, sandhill cranes continued migrating after dark more frequently in spring than in fall (Kessel 1979*b*). Observations on the ECRD support these findings, with cranes heard passing over the field camp well after dark on 28 April (3 flocks) and 5 May (1 flock) 1979, and on 29 April 1980 (1 flock). Cranes are also capable of flying at great heights, occasionally up to 4000 m (Walkinshaw 1949). Kessel (1979*b*) noted higher flight heights in spring than in fall among sandhill cranes passing through interior Alaska. Cranes on the ECRD occasionally flew to 1250 m but normally flew between 100 and 300 m altitude in spring ($\bar{X}$=276.2 m, SD=218.2). Flight heights were significantly higher (t=6.18, df=404, p=0.05) in spring than in fall for migrating crane flocks (excluding flocks making only local movements). Fall flocks average 160.54 m (SD=145.4) altitude and ranged from 15 to 1000 m.

Alerstam (1975) found migrating flocks of common cranes (*Grus grus*) rarely flew over 1000 m and consistently remained below the cloud base. On several occasions on the ECRD, cranes soaring and gaining altitude often entered clouds, but within minutes reappeared below the cloud base and remained at that level. On 30 April 1979 and 4 May 1980, however, cranes were heard high overhead but could not be located and were thought to be migrating above the clouds. Thus, flocks of cranes could also have been missed in spring as they flew above hearing or sight range, and continued migrating at night.

In fall, sandhill cranes first arrived on 22 August 1979 (flock of 11) and 19 August 1980 (flock of 2). Cranes were already present on the study area upon the field assistants' arrival on 27 August 1981. Local observers noted several flocks of 50-100 cranes each over Cordova on 16 August 1981 (G. Bucaria, P. Mickelson, pers. comm), the earliest recorded date. Numbers of staging cranes built to several hundred by the first week of September in all years, and peaked during mid- to late September (Fig. 5). After the first week of October in 1979 and 1980, crane numbers dropped below 100 birds and only stragglers remained past mid-October (latest, 6 on 20 October 1979). The last cranes observed in 1981 were a flock of 2 on 28 September, however, migration watches did not continue into October. In both spring and fall, timing of migration was very similar among all years. Peak numbers of cranes occurred later in

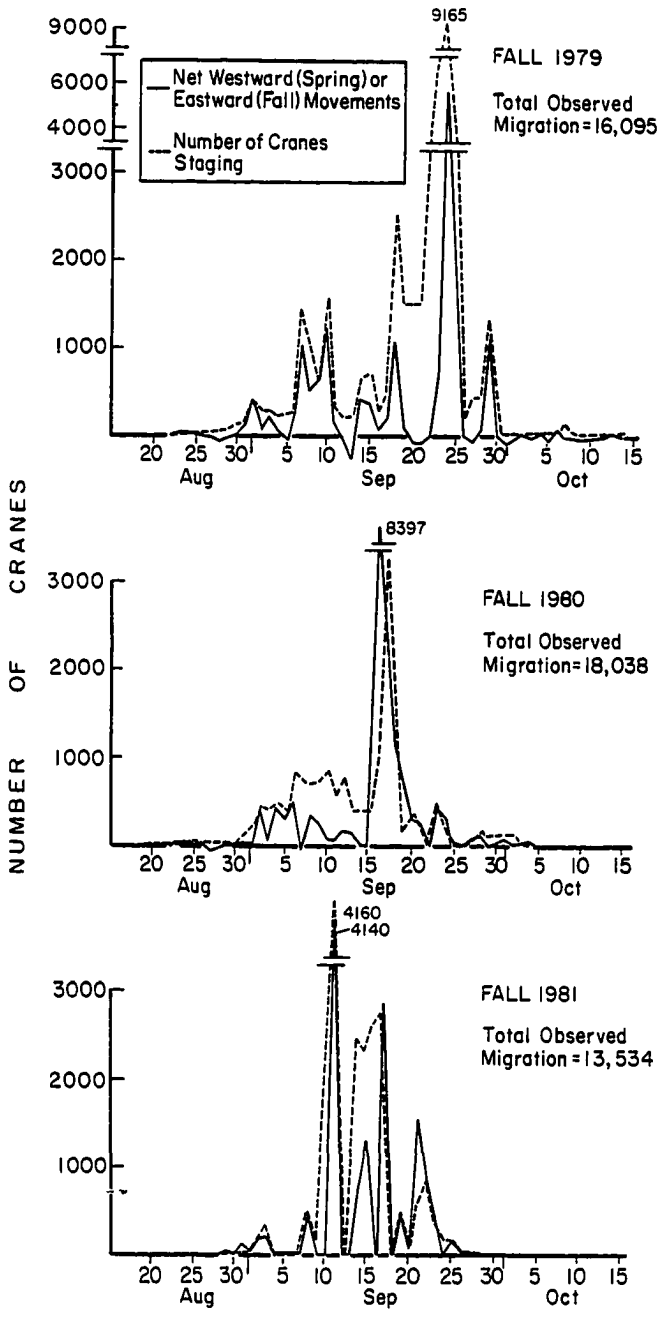

Figure 5. Timing of fall migration and staging activity as observed from camp sites on the eastern Copper River Delta.

fall of 1979 than in 1980 or 1981. Local commercial fishermen reported a number of flocks during late August before migration watches began in 1981, and few flocks remained by late September. Thus, 1979 may represent a slightly late year for migration while 1981 may represent a slightly early year. In all years however, by far the major passage of cranes through the ECRD occurred during the month of September (Fig. 5). Timing of crane migration near Delta Junction, Alaska, located approximately 425 km directly north of the ECRD, is very similar to this study with the exception of a 1-week lag in migration in spring at the interior site (Kessel 1979*b*).

Fall migration on the ECRD proceeded at a slower pace, covering almost 2 months, while migration in spring extended for only a 1-month period. Amount of staging activity varied between years as indicated by crane use-day levels in Table 3. Cranes spent roughly twice as much time on the ground during 1979 as in either 1980 or 1981. During fall 1979, only two small flocks of cranes were observed overflying the study area without stopping. Other cranes observed remained at least for 24 h and some up to 1 week to 10 days. Reasons for higher crane use in 1979 are unknown but may be related to lower food supplies in late summer near the breeding grounds. This would result in poorer pre-migratory condition of cranes (especially juveniles) and the need to rest and feed on the ECRD. Cooch (1958) speculated that geese leaving breeding areas with low fat reserves stopped more often on migration. In 1980,

nearly 8000 cranes overflew the ECRD on 16 September, however, staging occurred among most other flocks. Large flocks also frequently overflew the ECRD in fall 1981, although as indicated by crane use-days, staging activity was higher than in 1980.

Due to a lack of marked or otherwise identifiable individuals, the duration of stay of individual crane flocks can only be estimated. By observing arrivals and departures and daily counts of cranes, staging activity could occasionally be monitored. The following illustrates a typical staging scenario on the ECRD as observed from 8-11 September 1981:

9/8 Several flocks of cranes, totalling 410 birds depart the study area from 09:00 - 10:00 ADT. Few staging cranes are observed in the afternoon. One flock of 33 cranes arrives from the west and moves to a roost site by 18:30.

9/9 Frequent rain showers occur throughout the day, with 127 cranes present on the study area by nightfall. No cranes are observed leaving the ECRD.

9/10 Many small flocks totalling 1385 cranes arrive from the west and land at various points across the ECRD. Many land with other staging cranes near Russian River Slough. Most flocks of cranes fly north to roost near Martin River, but again no cranes are seen leaving the ECRD.

9/11 Arrivals during the afternoon or evening of 10 September swell roosting crane numbers to over 4000. Cranes fly south from roost sites to meadows near the spruce islands to preen and feed. Clearing skies and partial sunshine occurs by 09:00 with probably all cranes departing to the southeast after circling and gaining altitude on air thermals. A total of 4140 cranes are counted departing the study area.

In this example, most cranes stayed for 24 h or less, others for 2-3 days. Weather conditions probably played a major role in staging activity in this instance, but on other occasions it had little effect, as will be discussed in the following section.

When compared to other known staging areas of sandhill cranes, relatively little staging occurs on the ECRD. Radio-tagged greater sandhill cranes spent an average of 12 days (range=1-17 days) during spring and 9 days (range=6-23 days) in fall on the Jasper-Pulaski staging site in northwestern Indiana (Toepler and Crete 1979). Cranes that stage in spring on the Platte River in Nebraska spent an average of 26.2 and 31.7 days in 1978 and 1979 respectively, according to telemetry studies there (Krapu 1981). Munro (1950) and Stephen (1967) also suggest that fall staging activity is substantial at Last Mountain Lake, Saskatchewan, but they do not provide specific estimates of the amount of time spent there by

individuals or flocks. During fall, the ECRD is probably the most heavily used staging area of sandhill cranes along the Pacific coast, and in some years (e.g., 1979) it appears to be an essential staging area for almost all cranes passing through the North Gulf Coast region. Though duration of stay for individual cranes may be relatively short, staging probably serves essential physiological and social functions for cranes, including needed rest periods, addition of fat reserves or protein supplies, and reunification of family groups (Krapu 1981, Lovvorn and Kirkpatrick 1981). From a population perspective, cranes are present on the ECRD for almost 3 months during the relatively treacherous periods of migration, a time especially stressful for young of the year. Therefore, the value of staging stopovers in the annual cycles of sandhill cranes may be substantial.

The maximum total number of sandhill cranes actually observed passing the observation tower during fall was 18,038 cranes in 1980 (Table 3). The field camp in 1981 was in a less centralized location on the study area (Fig. 2), and flocks following the barrier islands were probably frequently missed. Persistent bad weather may have contributed to fewer birds seen in fall 1979. Approximately 20,000 sandhill cranes are estimated to have passed by the field camp in fall 1980; totals are adjusted for time spent away from the observation tower. Islieb and Kessel (1973) previously reported up to 500,000 sandhill cranes migrating through the ECRD, but this figure

is now believed to be an over-estimate (M.E. Islieb pers. comm.). Kessel (1979*b*) has similarly observed more cranes during fall migrations in interior Alaska than in spring.

Fall migration of lesser sandhill cranes in Canada and the northern United States proceeds at a more leisurely pace than spring migration, with heaviest use of northern staging sites in Saskatchewan and North Dakota in fall (Munro 1950, Buller 1967). Staging areas for lesser sandhill cranes closer to the wintering areas, such as the Platte River Valley in the Central Flyway and Malheur N.W.R. in the Pacific Flyway, receive higher use in spring but conversely little use in fall (Krapu 1981, C.D. Littlefield pers. comm.). The relatively northern ECRD staging area reflects the pattern seen in Saskatchewan and North Dakota, with higher use in fall than in spring. Cranes probably need to rest and/or feed more during the early stages of migration, while tending to "push-on" to their final destinations later in migration.

B. Weather and Migration

The effects of weather on bird migration have been extensively reviewed by Richardson (1978) and more specifically for common cranes by Alerstam and Bauer (1973) and Alerstam (1975). The position of the ECRD along the exposed Gulf of Alaska coast subjects the area to frequent severe weather systems originating in the

northern Pacific Ocean. Sandhill cranes, being primarily fair-weather migrants (Walkinshaw 1973, Nesbitt 1975*b*, Toepler and Crete 1979), were often forced to stage on the study area by foul weather conditions, particularly in fall.

Headwinds are particularly prominent in reducing numbers of migrants aloft (Richardson 1978) and inhibiting crane migration (Alerstam and Bauer 1973, Kessel 1979*b*). Cyclonic storms originating in the Gulf of Alaska often produce strong (25-65 km/h) southeasterly winds and heavy rain in fall, conditions especially poor for migrating cranes, which must follow a southeasterly course after leaving the ECRD. Figure 6 illustrates a comparison of mean daily wind speeds at the Cordova FAA weather station and major crane departures from the ECRD during 1979 and 1980. Winds are predominantly from the east or southeast in fall on the ECRD (Hawkings in prep.), so high wind speed values usually indicate unfavorable headwinds for cranes. Like hawks and vultures, cranes utilize rising warm air currents, known as thermals, to gain altitude immediately preceding and periodically during migration (Walkinshaw 1949, Alerstam 1975). Thermals are well developed on cool days following a period of warm weather, especially with low to moderate wind speeds (Cone 1962). During major fall storms on the ECRD, air temperatures were relatively warm (9-12°C) due to airflow from the ocean, while clear, calm nights usually brought colder temperatures (0-6°C). As seen in Fig. 6, most crane departures took place on days with low wind

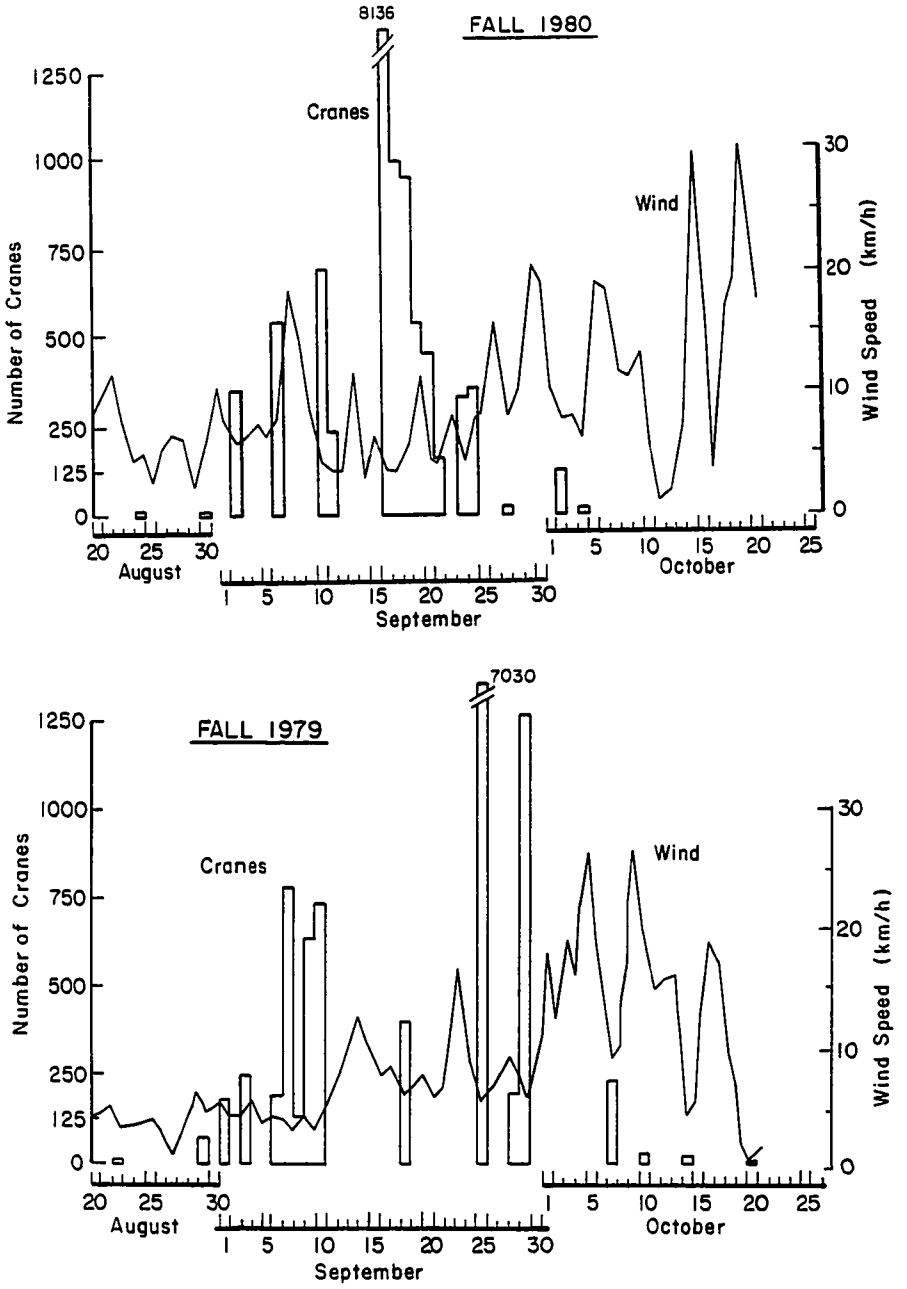

Figure 6. Wind speed (connected points) and numbers of cranes (histograms) observed departing the eastern Copper River Delta in fall 1979 and 1980.

speeds and also usually during clearing or clear skies. Thermal updrafts can form in many ways but probable patterns on the ECRD may involve updrafts along mountain ridges, or along sea-breeze fronts, where clear skies permit sunlight to heat air over land more than air over adjacent cold waters (Cone 1962). Thus, cranes grounded on the ECRD by stormy weather almost invariably departed if skies cleared during the night, with sunlight the following morning creating updrafts along the seaward sides of the Ragged Mountains.

In contrast to other diurnal migrants which depart early in the morning (Richardson 1978), cranes usually are not aloft until mid-morning when air thermals have developed. Most cranes that departed the ECRD after staging for 24 h or more, left between 09:00 and 11:00 ADT ($\bar{X}$=09:55). A notable exception occurred on 17 September 1981 when 1200 cranes had departed by 06:00 under clear and calm conditions with heavy ground fog, which possibly precluded landing once they left their roost sites. Times of departure on the ECRD compared closely with those of cranes departing north from Florida, which left between 09:00 and 12:29 EDT (Nesbitt 1975*b*). Cranes occasionally departed the ECRD on cloudy days. A flock of 455 left during the day on 19 September 1981 with a 100% overcast sky, and 160 departed during light rain but improving weather conditions on 21 September 1980. In all cases, winds were light during departure.

Tailwinds are particularly favorable for crane migrations and typified days of heavy flights across the Baltic Sea (Alerstam and Bauer 1973) and eastern North America (Toepler and Crete 1979). In the northern hemisphere, air moves clockwise around highs and counterclockwise around lows. High pressure systems are very rare over the Gulf of Alaska in fall, but when they occur, they often produce favorable winds for crane migration along the North Gulf Coast. From 13-15 September 1980, a persistent low over the Gulf produced light rain, drizzle, and fog along the coast. Migrating cranes were apparently grounded at various points in southcentral Alaska, as were 400 on the ECRD. On 16 September, clear skies and northwest winds produced by an approaching high provided strong tailwinds, and nearly 8000 cranes passed through the study area without stopping. Over the next 2 days, another 4000+ cranes also took advantage of the strong (20 km/h) tailwinds and migrated past the ECRD, although half of these stopped overnight on 17 September. This may represent a fairly unique weather situation as noted by Hawkings (in prep.), as northwesterly winds occur very rarely on the ECRD in fall, especially for several days at a time.

While surface winds are often good indicators of winds aloft, wind speed and direction at higher altitudes may vary, with winds frequently more rapid and directed to the right of surface winds (Richardson 1978). Differences between surface winds and winds aloft may explain why 10 flocks of cranes totalling over 1500

individuals, migrated northwesterly at 300-500 m on 26 April 1980 in seemingly strong (20 km/h) surface crosswinds from the northeast.

Heavy precipitation suppresses migration of cranes (Alerstam and Bauer 1973), but examples of cranes migrating through rain, snow, and even fog were reported by Kessel (1979*b*). Cranes occasionally flew through rain showers on the ECRD, particularly in spring, but severe storms with strong winds and heavy rain always grounded cranes. Rain showers, often heavy at times, persisted all day on 26 April 1980, but over 1500 cranes moved through the ECRD throughout the day. In fall, cranes frequently flew through rain showers over the WCRD in order to stage on the ECRD.

Temperature and barometric pressure may also affect migration of birds (Richardson 1978). Warm temperatures in spring are thought to initiate some migrations while cool temperatures in fall have the same effect. Kessel (1979*b*) noted flocks of cranes flying in poor weather during fall when barometric pressures at their destination were rising, indicating improving weather. Petersen et al. (1981) found rising barometric pressures, warm temperatures, following winds, and good visibility were all correlated with crane migrations at Yakutat, Alaska. Temperature and pressure changes likely also affect crane migrations on the ECRD. Rising barometric pressure east of the ECRD on 20 September 1981 (Deutscher Wetterdienst 1981) may explain the departure of 100 cranes from the study area under 100% overcast skies and occasional light rain.

Few birds have been recorded initiating migrations, then returning because of unsuitable weather conditions (Richardson 1978). On 15 September 1981 flocks totalling almost 1000 cranes circled and soared to 600 m near the Ragged Mountains as if to leave the study area, but descended 15 min later, apparently finding weather conditions unfavorable for migration. At that time, 100% cloud cover at 1000 m and slight southeast winds seemed to indicate weather was not favorable, and cranes staged for 2 more days. Smaller groups of cranes were observed conducting this "testing" behavior in fall of all years.

Weather undoubtedly has profound effects on crane migration and staging on the ECRD, particularly in fall when cranes do not seem to "push-on" as rapidly as they do in spring. Grounding due to poor weather can explain some staging but is not the only cause. As exhibited in fall 1979, even during periods of good migration weather, virtually all flocks of cranes arriving on the study area stopped there for at least 24 h. This seems to indicate other reasons, probably physiologic in nature, induced cranes to stage on the ECRD. In 1980 and 1981, staging during fair weather also occasionally occurred, but favorable tailwinds and clear or partly cloudy skies usually pushed cranes past the ECRD. In all years however, the majority of cranes successfully completed migration through the ECRD from mid-April to mid-May, and during the month of September. Fair weather at these times almost always produced some crane migration in the CRD region.

C. Flock behavior

During most of the year, from late summer to spring, sandhill cranes aggregate into sizeable flocks. Due to their gregarious nature, the presence of a crane flock in an area often attracts other flocks to land nearby. Therefore the decision to rest and feed by one flock may influence several other flocks to do likewise. Particularly in spring, flocks of cranes passing within sight or hearing of another flock on the ground on the ECRD became undecided, with part of the flock aloft continuing on while another portion descended and joined the other cranes on the ground. This tends to indicate that the decision of a flock early in a movement to stage on the ECRD can also have an affect on the level of staging activity that will occur that day and in following days.

While staging, the social organization within flocks can affect distribution of birds. Miller and Stephen (1966) found large crane flocks appeared to be composed of smaller groups functioning somewhat independently within the aggregation. In fall on the ECRD, family groups were usually associated with a larger flock, but during daytime feeding they often separated and drifted away from the central group. During flights to roosting sites or to continue migration, family groups again reassociated with a flock. Overall, flock sizes remained fairly constant on the ECRD (Table 4), with large aggregations occurring only during *en masse* departures from the study area.

Table 4. Flock sizes of migrating sandhill cranes observed on the eastern Copper River Delta.

Migration period	Mean	SD	Range
1979			
Spring	82.7	80.5	2-500
Fall	90.1	194.3	1-7000
1980			
Spring	83.7	116.7	2-600
Fall	91.2	118.8	1-1000
1981			
Fall	86.6	107.7	1-2000

Family groups frequently remain together throughout the winter, and ties with the juvenile(s) are broken when the pair returns to the nesting territory (Walkinshaw 1973). On 23 April 1980, high-pitched juvenile voices were heard among a flock of 110 cranes, and several 3-bird groups were noticeably separated from the main flock. This indicates some family groups also remain intact among spring migrants on the ECRD.

On occasion, sandhill cranes have been known to associate with other bird species, particularly geese (Nesbitt 1975*a*). On the ECRD, cranes only rarely migrated with geese but frequently associated with staging goose flocks on the ground. On 7 May 1979, 4 cranes flew in V-formation with a flock of 53 cackling Canada geese (*B. c. minima*). Four snow geese (*Chen caerulescens*) arrived on the study area in formation with 47 cranes on 4 September 1980. Cranes were observed landing near feeding dusky Canada geese on several occasions during fall staging. Cranes could only infrequently be seen on the ground from the observation tower so the prevalence of association with geese cannot be estimated. The presence of geese may indicate a safe landing site for crane flocks and vice versa. Small flocks of cranes (<10 birds) tended to associate with geese more often than large (>50 birds) flocks. Dusky Canada geese occasionally landed near 3 crane decoys, and near feeding cranes on several occasions. Aggressive encounters between cranes and geese were few, as the two species avoided each other, even though they occasionally fed close together.

II. MIGRATION ROUTES

Most lesser sandhill cranes breeding in Alaska migrate through the Central Flyway, remaining east of the Rockies and wintering in Texas, New Mexico, Arizona, and Mexico. This mid-continent population of lesser sandhill cranes has recently been estimated by Krapu (1981) to be nearly 350,000 birds, as indicated from population estimates taken along the Platte River spring staging grounds. Kessel (1979*b*) has counted nearly 200,000 sandhill cranes migrating through eastcentral Alaska in fall. Lessers banded on wintering grounds and during spring migration in the Central Flyway have been resighted on breeding areas in northern Canada, Alaska, and Siberia (Huey 1965, Boise 1981, T. Tacha pers. comm.). Lesser sandhills banded on breeding grounds on the Yukon-Kuskokwim Delta, Alaska, have been resighted at Central Flyway staging areas and wintering grounds (Boise 1981).

At the time this study was initiated, sandhill cranes staging on the Copper River Delta were thought to either join the Central Flyway birds somewhere along their migration route, or remain in the Pacific Flyway and migrate to and from California wintering grounds. A population of lesser sandhill cranes has long been known to winter in the Central Valley of California (Grinnell and Miller 1944), and as evidenced from prehistoric bone fragments, the subspecies has probably wintered there since long before recorded

history (Littlefield and Thompson in press). This wintering population has remained relatively constant at 20,000 to 25,000 cranes (Lewis et al. 1977, Littlefield and Thompson in press). It has been suggested by Walkinshaw (1949) and by arrows on a distribution map in Lewis et al. (1977) that this population migrates north through British Columbia. Few sightings of large migratory flocks of lesser sandhill cranes and no banding or color-marking of lessers in the Pacific Flyway existed to confirm a population of lessers utilizing only Pacific Flyway migration routes.

A. Color-marking

The inaccessibility of the ECRD, lack of manpower, and the relatively short staging times of sandhill cranes prohibited use of labor-intensive and bulky trapping gear for capturing sandhill cranes. The two methods of capture tried on the ECRD, night-lighting and snaring, resulted in two cranes caught but only one banded and color-marked. Attempts to night-light cranes took place on 4 nights in September 1979. Only on nights with 100% overcast skies and with cranes roosting on nearby mudflats was night-lighting attempted. On the evening of 21 September 1979, during a heavy rain shower, all members of a flock of roosting cranes flew off when approached with the light, except for 1 crane which seemed blinded and confused by the light. This crane was captured with a

long-handled net. An aluminum leg band was placed on its right leg and a yellow aluminum neck collar on its neck. To date, this bird has not been resighted. A crane was ensnared briefly by the monofilament snares placed near the crane decoys on 25 September 1979. It soon broke the noose from its leg after a short struggle and flew off. Staging cranes were usually too nervous to approach closely on roost areas with strong lights on the ECRD. They often walked over the monofilament snares without being trapped. Lewis (1974) also found large roosting flocks of cranes could not be approached easily with night-lights, and also reported little success with snares (Wheeler and Lewis 1972). Juvenile sandhill cranes however, were easily caught with night-lights on nesting areas in Idaho (R.C. Drewein, pers. comm.).

During 1979, no marked sandhill cranes were observed among over 4000 cranes seen close enough to detect color markers such as wing tags or neck collars. Over 1500 sandhill cranes had been marked in the Central Flyway by spring of 1979 (Ramakka 1979, Tacha 1981), and 128 lesser sandhills were marked on the Yukon-Kuskokwim Delta, Alaska by 1979 (Boise 1979). In light of this extensive color-marking, cranes staging on the ECRD were thought to possibly belong to a separate population. Since most migratory waterbirds appearing on the CRD are Pacific Flyway migrants, it seemed likely that the cranes may also be using a Pacific Flyway route.

After 5 successful attempts at capturing cranes with rocket nets at Merced NWR, California, 43 lesser sandhill cranes were marked during February and March 1980. Eight other shots with rocket nets failed due to rocket misfire, faulty wiring, lack of sufficient amounts of rocket propellent, poor rocket angle, and escape of cranes beneath the extending nets. Other problems encountered at the trap sites included disturbance from nearby hunters and refuge visitors, low numbers of cranes on the refuge in 1980, frequent heavy fog which obscured visibility of the trap site, consumption of the corn bait by blackbirds and geese, and failure of bait and decoys to attract cranes until mid-February. Trap sites in harvested cornfields were ideal in that they provided abundant plant materials for camouflage of the nets, and were used daily by cranes for feeding. Ramakka (1979) also noted cranes failed to accept corn bait until late February at trap sites in western Texas. Depletion of other food sources and increased food consumption in preparation for migration may explain the increased attraction to bait by late winter. Greater numbers of lesser sandhill cranes could possibly be captured in central California by strictly following the suggestions of Ramakka (1979), delaying trapping until late winter, and utilizing trap sites at several crane concentration areas in California, including Merced NWR.

Table 5 summarizes resightings of the lesser sandhill cranes marked with red neck collars and leg bands in California. Marked

Table 5. Resightings of lesser sandhill cranes color-marked in February and March 1980 at Merced National Wildlife Refuge, California.

Date sighted	Location	Collar code	Observer(s)
2-3 March 1980	near Burns, Oregon	EE02	D. Paullin, S. Thompson
11 March 1980	near Burns, Oregon	?	S. Thompson, C. Littlefield
22 March 1980	near Burns, Oregon	?	S. Thompson, C. Littlefield
13 April 1980	(2) near Bonanza, Oregon	? ?	C. Ely
30 April 1980	ECRD, Alaska	?	D. Herter, D. Haynes
11-14 May 1980	ECRD, Alaska	EE30	D. Herter, D. Haynes
10 Sept. 1980	ECRD, Alaska	?	D. Herter
21 Sept. 1980	ECRD, Alaska	?	D. Herter, D. Haynes
15-20 Sept. 1981	(2) Carrizo Plains, San Luis Obispo Co., Calif.	? ?	B. Hartwell
winter 1981	Merced NWR, Calif.	EE31	R. Fuller
8 March 1981	near Bonanza, Oregon	EE10	C. Ely
21-25 March 1981	near Burns, Oregon	EE30	S. Thompson
17 Sept. 1981	ECRD, Alaska	?	D. Herter, R. Burgess
17 Sept. 1981	ECRD, Alaska	EE41	D. Herter
September 1981	near Gustavus, Alaska	?	C. Matkin

cranes sighted in Oregon were at spring stopover points in the Klamath Valley and near Malheur NWR. Up to six different marked cranes were sighted on the ECRD study area in 1980 and 1981. These were the only color-marked cranes observed on the ECRD out of 1200 seen close enough to detect markers in spring 1980, and of 6500 and 5000 examined in fall 1980 and 1981, respectively. One marked crane was observed at a fall stopover point near Gustavus, in southeastern Alaska, and 3 birds were observed at wintering areas in California during 1981.

All resighted birds were members of large flocks and appeared to be accepted members of their groups. After the initial capture at Merced NWR, marked birds exhibited some abnormal behavior for several days, including roosting alone or at the edge of a flock and reluctance to feed or fly. One bird inserted its lower mandible inside the collar but could not remove it by its own struggling and had to be recaptured. In a few months however, marked cranes exhibited normal behavior, were observed winning agonistic encounters with other flock members, and appeared to be able to feed normally. Crane EE41, observed in fall 1981 on the ECRD, was paired with an unmarked crane and was observed giving food items to a juvenile, presumably its own chick. Boise (1981) noted yellow neck collars may interfere with normal pairing and breeding of lesser sandhills. Two cranes with red neck collars sighted on the Carrizo Plains in California appeared to be paired as they separated from a large

flock and performed courtship displays together (B. Hartwell pers. comm.). These birds may have been paired before they were marked, however.

To date, all resightings of cranes marked at Merced NWR have occurred within Pacific Flyway migration routes (Fig. 7). Banding records from the Bird Banding Laboratory in Laurel, Maryland indicate no exchange of marked or banded birds between mid-continent populations and Pacific coast populations of lessers. As in other populations of birds of the same subspecies, however, some interchange may occur between Pacific Flyway and mid-continent lesser sandhill cranes on an annual basis, possibly between adjacent breeding areas in Alaska. Banding thus far indicates ECRD cranes belong to a distinct Pacific Flyway population of lesser sandhill cranes.

B. Route Delineation

Pacific Flyway lesser sandhill cranes winter in two separate areas of California; a small group of about 1400 near Red Bluff in northern California, and the main population of about 20,000 to 23,000 birds throughout the Sacramento, San Joaquin, and the smaller neighboring valleys in central California (Littlefield and Thompson in press). These authors have further traced the migration routes of lessers through the contiguous Pacific coast states, where the main eastern segment migrates through northeastern California east

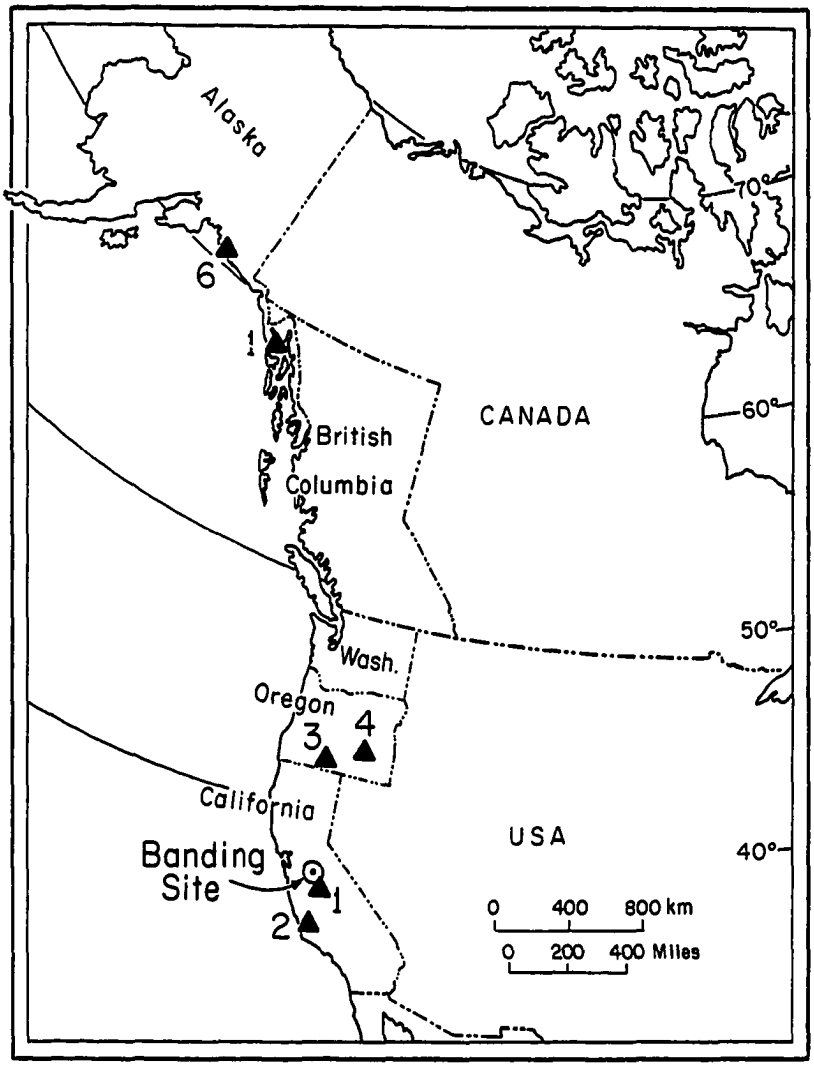

Figure 7. Resighting locations (1980-1981) of lesser sandhill cranes color-marked at Merced National Wildlife Refuge in February and March 1980. Numbers indicate number of marked birds sighted at each location.

of the Sierra Nevada Mountains, thence through eastern Oregon and Washington, east of the Cascade Mountains. Stopover points along this route are used most heavily in spring. Major use areas in recent years have been Malheur-Harney Lakes Basin, where up to 14,000 may be present in March of some years (Littlefield and Thompson in press). In eastern Washington, 2 major spring stopover areas occur in southeastern Lincoln County and near St. Andrews, Douglas County (Yocum and Hansen 1960; Rogers 1971, 1976, 1979, 1980). The smaller western segment of the population migrates west of the Cascade Mountains, through the Willamette Valley, Oregon, thence north through the Puget Sound area of Washington. The only major stopover area of this population is at Sauvies Island on the lower Columbia River, a site most heavily used in fall (Baldridge and Crowell 1966, Crowell and Nehls 1970, Littlefield and Thompson 1979, Mattocks and Hunn 1980). Occasionally, migrating lessers stray farther east or west where numbers may appear in northwestern Nevada, western Idaho, and the Pacific coast of Washington (Crowell and Nehls 1974, Drewein et al. 1976, Littlefield and Thompson in press).

In Canada and Alaska, migration records of lesser sandhills are most prevalent in the fall. Breeding areas of Pacific Flyway lessers are not known at present but circumstantial evidence points toward the Cook Inlet and Bristol Bay lowlands as likely areas. Banding information revealed that cranes breeding on the Yukon-

Kuskokwim Delta, at least in the Old Chevak area, migrate through the Delta Junction area of interior Alaska and continue south through the Central Flyway (Boise 1981). Cranes breeding north of there most likely also use interior Alaska routes and continue through the Central Flyway. Sandhill cranes breeding in Siberia migrate across the Bering Strait at its narrowest point near the Diomede Islands (Bernard 1923, Breckenridge and Cline 1967, Flock 1972). They continue eastward in fall across the southern Seward Peninsula (Drury 1976, Kessel and Gibson unpubl. records) and often stop on lowlands along Norton Bay (Shields and Peyton 1978). From there they fly inland (L.J. Peyton pers. comm.), where large numbers are seen near Nulato (M. Stickman pers. comm.), and then probably join other migrants as they near Delta Junction.

Sandhill cranes have been regularly observed in summer, and breeding has been noted at many locations along the entire length of the Alaska Peninsula to Unimak Island in the far eastern Aleutians (Murie 1959, Hayward et al. 1977, Gill et al. 1977). Observations of scattered small groups and pairs may indicate a few breed in the Aleutian Islands as far west as Agattu and Attu Islands (Byrd et al. 1974, Kessel and Gibson unpubl. records). Favorable breeding habitat and breeding cranes occur westward along the north shore of Bristol Bay to Kulukak Bay, and sparingly farther west to Cape Peirce (Petersen and Sigman 1977, Conant et al. 1981). Breeding also occurs sparingly on Cook Inlet lowlands, from Redoubt Bay to

the lower Susitna River, and Kenai Peninsula lowlands (Conant et al. 1981; T.N. Bailey, M.A. Miller, and D.E. Timm, pers. comm.). Breeding population estimates of cranes, gathered during aerial waterfowl breeding pair surveys along Bristol Bay and Cook Inlet averaged 11,095 birds and ranged from 5180 to 21,380 cranes (Conant et al. 1981). Survey transects did not cover all probable Pacific Flyway lesser sandhill breeding areas, so population estimates are probably low. They are, however, within reason if 20,000 to 25,000 lessers are estimated to belong to the Pacific Flyway population.

Observations of sizeable migrating flocks of cranes have occurred at several points between breeding areas in Bristol Bay and Cook Inlet, and Washington state, mostly during fall (Fig. 8). Villagers at Kakhonak, on the south shore of Iliamna Lake, have annually noted concentrations of sandhill cranes passing eastward from near the village to Bruin Bay, on Kamishak Bay in Cook Inlet, during September. In mid-September 1979, approximately 10,000 cranes used this route in a 3-day period (A. Payne, fide S.O. MacDonald pers. comm.). Farther east, large flocks of cranes have been observed migrating in September over Homer in 1960 (Smith 1961) and 1981 (D. Curran pers. comm.). Flocks are observed annually over the Cohoe-Kasilof area (M.A. Miller pers. comm.) and Kenai NWR (T.N. Bailey pers. comm.) during late April and early May and again in mid-September to October (latest, 9 October 1974 at Soldotna). Flocks of 50-150 are occasionally seen in the Anchorage area during

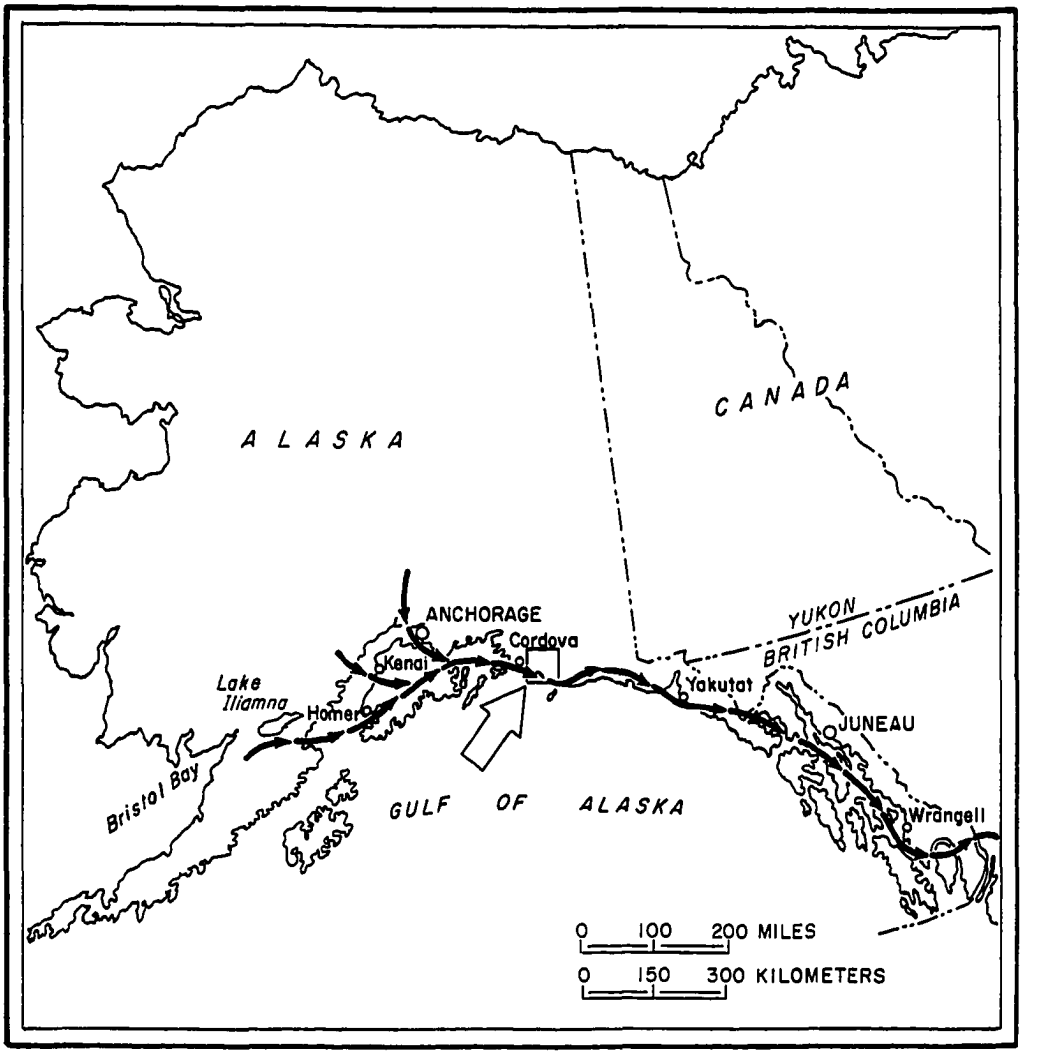

Figure 8. Fall migration pathways of Pacific Flyway lesser sandhill cranes through Alaska, as indicated by sightings of marked birds and observations of large migratory movements of cranes. Spring migration is essentially the reverse of fall. Arrow points to ECRD study area.

migrations (Ritchie et al. 1981, Kessel and Gibson unpubl. records), and an estimated 1000-1200 birds were on a field near Palmer around 1 October 1962 (Smith 1963). Flocks of 100's or 1000's may rest on the Portage Flats at the head of Turnagain Arm before passing east into Prince William Sound through Portage Pass (D.E. Timm pers. comm.). Other flocks fly over the Kenai Mountains to the south, on their way to or from, Prince William Sound (Smith 1961, 1963; Islieb and Kessel 1973). Cranes apparently fly directly over Prince William Sound to, or from, the CRD area (Islieb and Kessel 1973). In fall on the CRD, cranes fly over the marshes of the WCRD or follow the barrier islands and turn northward to stage on the ECRD. Departing cranes occasionally fly directly over the Ragged Mountains, but usually follow the lower coastline around Martin Point and Katalla Bay and thence eastward over the Bering River Delta. On 16 September 1980, almost 8000 cranes passed through the ECRD, but large numbers were not recorded at Yakutat until 17-18 September 1980 (Patten 1981, Petersen et al. 1981). These cranes apparently stopped somewhere east of the ECRD, perhaps the Bering River Delta, along the east side of Icy Bay, or the upper Yahtze River--sites where cranes have been known to congregate (Patten 1981, R. Gill pers. comm.). Migration watches conducted at Cape St. Elias, Kayak Island, recorded only one crane during watches in spring of 1977 and 1978 (Arneson 1980). Cranes seem reluctant to fly over large stretches of open water (Flock 1972, Alerstam

1975), so probably all flocks of cranes remain along the coastline once departing the ECRD.

Recent migration studies at Yakutat (Patten 1981, and Petersen et al. 1981) found sandhill cranes were fairly common migrants, with peak numbers of 69.92, 42.52, and 42.36 cranes/h on 24 and 26 April, and 4 May 1980, respectively, and over 4500 counted in September 1980. Migrating cranes were noted in the Yakutat area from 22 April to 4 May and 6 September to 4 October 1980. In fall, cranes were observed flying across Yakutat Bay, over the coastal mountains and Yakutat and Novatak Glaciers, up the Alsek River Valley, and thence southward toward Glacier Bay (Patten 1981). Flocks of 150 and over 200 cranes have been observed at Glacier Bay in spring and fall, respectively, with some fall staging on tidelands near Gustavus (Wik and Streveler 1968, C.O. Matkin pers. comm.). Over 9000 cranes were counted passing through the Gustavus area in fall 1981 (G. Streveler pers. comm.). Spring migration occurs both through Glacier Bay and along the outer coast where over 950 birds were counted moving north near Cape Fairweather in 1970 (Kessel and Gibson unpubl. records). Pathways through the Alexander Archipelago are not well defined and may vary from year to year. Sizeable flocks have been recorded over Icy Strait and Auke Bay near Juneau, over Keku Strait near the village of Kake, and on the Stikine River Delta near Wrangell (Kessel and Gibson unpubl. records). Large numbers were heard over Kake on 22 September 1972,

and a flock of 1100 flew over on 30 April 1972, but in some years no migration was observed there (Gibson 1972). Although most flocks merely pass by, up to 2000 cranes at a time may stage for a few days to 1 week on the Stikine River Delta in fall (R.E. Wood pers. comm.). Migrants are observed from 15 September to 15 October in most years with peak numbers recorded from 20-30 September. In fall 1979 over 11,500 were counted moving through the Delta. No movement of cranes was observed up the Stikine River Valley from 1974 to 1980 (R.E. Wood pers. comm.); rather, all flocks continued south and probably entered British Columbia along river valleys at the very southeast corner of Alaska. From 26 April to 6 May 1974, 2000-3000 sandhill cranes passed down the Chickamin River Valley, east of Ketchikan, on northward migration (MacDonald and MacDonald 1975).

A pair of cranes with a fledged chick observed on the WCRD in late July 1977, and nest attempts on Kupreanof and Prince of Wales islands, southeastern Alaska (Gabrielson and Lincoln 1959, Kessel and Gibson unpubl. records) indicate a few pairs of cranes may stop and breed along the migration route in southcentral and southeastern Alaska.

From Alaska, crane flocks are next reported in the Smithers, British Columbia (B.C.) area where groups of over 100 birds have been seen in spring and fall over Francois Lake (Munro 1947; Fig. 9). Migration dates there were from mid- to late April and during the month of October. Paul (1959) reported cranes were regular migrants

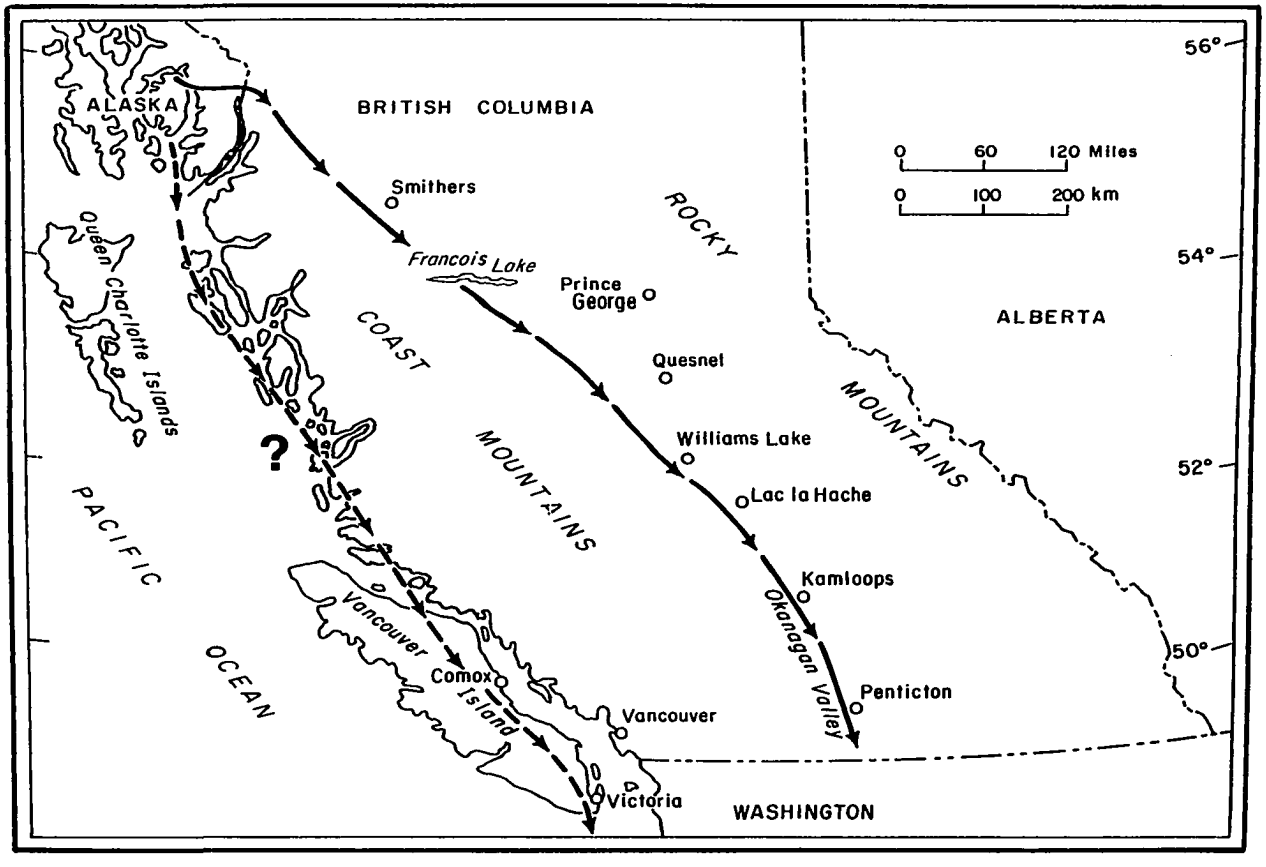

Figure 9. Fall migration pathways of Pacific Flyway lesser sandhill cranes through British Columbia, as indicated by observations of large migratory movements of cranes. Spring migration is essentially the reverse of fall. Dashed line indicates probable path of the western segment of the population.

at Chezacut, 130 km west of Williams Lake, B.C., but not farther west at Kleena Kleene. Migration of lessers has also been noted in the Cariboo district near Quesnel and Williams Lake (Brooks 1903, Rogers 1960). Walkinshaw (1949) reported cranes were abundant migrants in the "old days" through the Lac la Hache Valley in spring, where great flocks flew overhead for weeks. About 1000 cranes were counted at Knutsford, near Kamloops on 13 October 1963 (Rogers 1964), and other movements have been reported from the Kamloops area (Rogers 1963). Migration of large flocks of cranes through the Okanagan Valley in British Columbia and Washington is well documented from Penticton, B.C., to Okanagan, Washington (Cooke 1914, Brooks and Swarth 1925, Campbell and Meugens 1971, Myres and Cannings 1971, Rogers 1981). Movements occur in mid- to late April and again in late September and October. Both large and small subspecies were grounded during a windstorm at Okanagan Landing, B.C. on 4 October 1917 (Munro 1919).

A smaller migration of the western segment of Pacific Flyway lesser sandhills probably follows the coast of B.C. after separating from the main movement in southeast Alaska. Numbers of cranes were reported going over Comox, on Vancouver Island, B.C., from late March to mid-April (Flahaut 1950, 1952; Flahaut and Schultz 1954), and were seen migrating at other eastern Vancouver Island sites (Brooks and Swarth 1925, Alford 1928, Jarvie and Jarvie 1970). Sandhill cranes were rare migrants along the outer coast of Vancouver

Island (Hatler et al. 1978), and are regular in small numbers in spring and fall near Vancouver, B.C. (Cumming 1932).

Sandhill cranes breed throughout British Columbia to the latitude of Prince George, including Vancouver Island and the Queen Charlotte Islands (Brooks and Swarth 1925; Young 1927; Darcus 1930; Laing 1935; Munro 1936, 1947; Campbell et al. 1972). Littlefield and Thompson (1979) suggest cranes nesting in central B.C. may be Canadian sandhill cranes (*G. c. rowani*), while more southerly birds seem to be greaters (*G. c. tabida*).

More observation records are needed for lesser sandhill cranes along Pacific Flyway routes to better delineate pathways. Migration routes may change slightly from year to year, between seasons, and depending on weather factors. Common crane migration paths vary over open water, depending on wind direction, but vary little overland, suggesting cranes make use of landmarks during migration (Alerstam 1975). Consistent sightings of migrating lesser sandhills at various points along the Pacific Flyway migration route seem to support his conclusions. The few sightings of staging cranes in southeast Alaska and British Columbia may indicate cranes often overfly these areas. Continuous flights of 584 km were recorded for greater sandhill cranes over the southeastern U.S. (Toepler and Crete 1979), and Lewis (1974) estimated some lesser sandhills may make nonstop flights in fall of approximately 1400 km from North Dakota to Oklahoma.

Identification of breeding grounds and major stopover areas are considered primary research needs for Pacific Flyway lesser sandhill cranes (Kramer et al. 1981). Color-marking crane chicks on suspected breeding areas, and resighting marked birds on the "more-peopled" wintering grounds may facilitate determination of nesting areas. Telemetry studies and ground observation at staging and migration stopover areas would aid identification and eventual protection of important use areas.

III. SUBSPECIES IDENTIFICATION

A. Body Measurements

Previous authors have not identified the sandhill cranes passing through the Copper River Delta to subspecies (Islieb and Kessel 1973). Gabrielson and Lincoln (1959) state that lesser sandhills nest in areas of Alaska that are likely breeding areas for the Pacific Flyway population, and others identify lessers on the wintering grounds in California (Lewis et al. 1977, Littlefield and Thompson 1979). However, the recently described Canadian sandhill crane (*G. c. rowani*), which nests in the northern Prairie Provinces, may also be present in the Pacific Flyway (Aldrich 1979). Table 6 summarizes all measurements taken on collected or hunter-bagged cranes on the ECRD during all three study years, and of live cranes trapped at Merced NWR, California in February 1980. Most cranes measured on the ECRD fall within the ranges given for the lesser sandhill crane by Aldrich (1979), Johnson and Stewart (1973), Lewis (1974), and Walkinshaw (1949), but the means of all measurements for both adult males and females are slightly greater than means given for *G. c. canadensis*. These means are lower than those given for the Canadian sandhill crane (*G. c. rowani*), a subspecies intermediate in size between greater and lesser sandhill cranes. Based on these previously reported measurements of subspecies,

Table 6. Weights (gm) and measurements (mm) of Pacific Flyway lesser sandhill cranes.

mean range (sample size)	Weight	Total length	Bill from posterior nares	Exposed culmen	Wing chord	Tarsus	Middle toe
Alaska (ECRD)							
Adult males	3770 3050-4500 (15)	944 870-1010 (15)	76 67-88 (16)	99 94-105 (5)	474 440-507 (15)	198 165-220 (17)	79 72-85 (17)
Adult females	3540 2950-4100 (9)	911 850-965 (10)	74 67-85 (13)	95 86-107 (8)	456 420-490 (11)	190 177-220 (12)	78 74-82 (12)
Adults	3740 2950-4500 (30)	933 850-1010 (31)	74 62-88 (39)	95 82-107 (22)	460 420-507 (37)	195 165-220 (36)	79 72-87 (38)
Juvenile males	3090 2460-3450 (3)	890 820-980 (4)	59 53-64 (4)		433 390-460 (4)	185 160-198 (3)	76 74-79 (4)
Juvenile females	2300 (1)	800 (1)	52 (1)		410 (1)	165 (1)	72 (1)
Juveniles	2980 2300-5100 (30)	885 800-980 (31)	60 52-65 (39)	80 79-81 (22)	444 390-495 (38)	193 165-220 (36)	79 72-79 (38)
California (Merced NWR)							
Adults	3580 3300-5100 (24)		72 65-85 (17)	90 87-94 (3)	460 415-510 (17)	188 165-220 (17)	78 75-83 (14)

I subjectively classified individual adult cranes as either *canadensis* or *rowani*, with the result of 31 birds classified as *canadensis* and 8 as *rowani*. No cranes, however, had all measurements exclusively within the *rowani* range, particularly in regard to bill measurements, but the highly distinguishing wing and tarsus lengths indicated the possible presence of *rowani* specimens. Several birds fell totally within the ranges given for *canadensis* however, and weights of cranes taken on the ECRD fall below most of those given for the "Prairie Intermediates" (*rowani*) in Walkinshaw (1949). Almost all cranes examined in fall on the study area were very fat, with high deposits of both subcutaneous and body cavity fat, and were therefore near their peak weights. Mean weights and measurements of lesser sandhills banded in California are less than those of ECRD cranes, though several do also fall within the ranges given for *rowani*. These birds could not be sexed so the data are not conclusive for *rowani*, however many specimens were definitely lessers based on weights and body measurements.

B. Track Measurements

Track measurements from the spring migration period of 1979 and 1980 are summarized in Figure 10. A chi-square analysis ($\chi^2=36.01$, df=20, $P\leq0.05$) revealed this distribution to be non-normal, and subsequent tests revealed a skewness coefficient of -0.054 and a

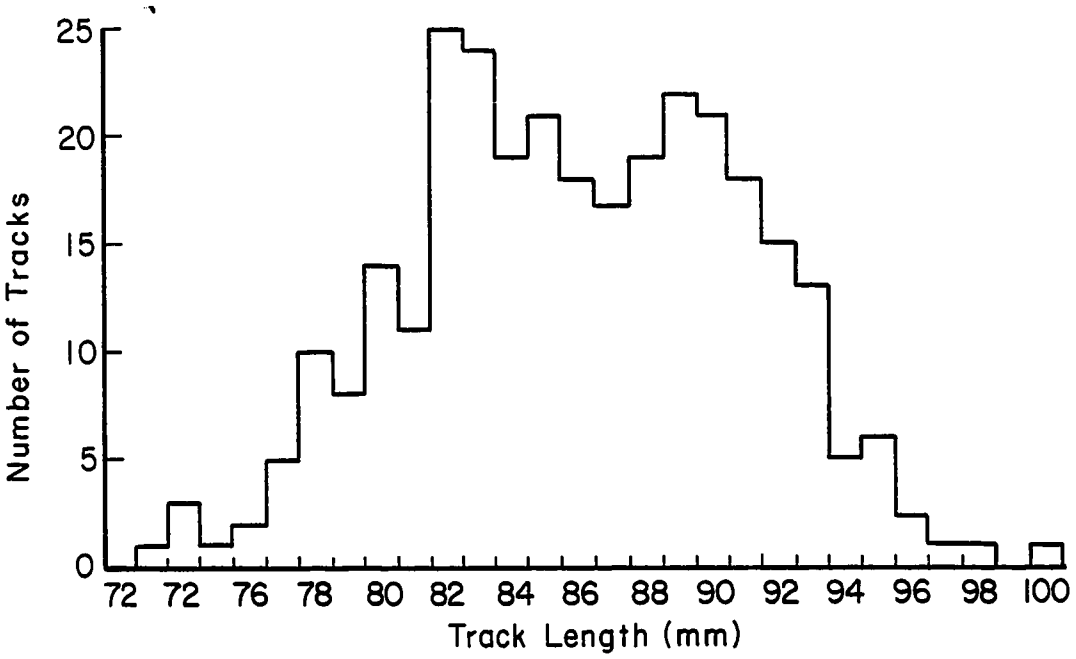

Figure 10. Frequency diagram of track imprint measurements taken in spring 1979 and 1980 on the eastern Copper River Delta.

kurtosis coefficient of -2.165. The strongly negative kurtosis coefficient indicates the distribution is platykurtic, suggesting there are two normal distributions with equal variances but different means within the overall distribution. These two normal distributions could conceivably result from male and female track distributions, or of two subspecies populations. While the latter case may be possible, it seems reasonable that the platykurtic distribution was caused by differences between male and female crane track sizes. The means of male and female middle toe lengths were only 10 mm apart and the chi-square test revealed the distribution to be only slightly non-normal. Tacha (1981) also noted females were consistently smaller than male sandhill cranes, and felt they warranted separate measurement analyses by sex.

Of 302 tracks measured on the ECRD in spring, average length was 85.9 mm and ranged from 73 to 100 mm. As with body measurements, track measurements of cranes taken on the ECRD averaged slightly larger than the mean size reported for lesser sandhill cranes (83.2 mm for males, 81.0 for females; Lewis 1974) but smaller than Canadian sandhill crane tracks ($\bar{X}$=88.8 for females). Tracks of 96 to 99 mm in length are reported to indicate *G. c. rowani* specimens (Guthery 1975). Five of the tracks I measured on the ECRD fell within this range. While it is possible there are both *G. c. canadensis* and *G. c. rowani* populations staging on the ECRD, there is likely only one population of lesser sandhill cranes which are

larger than the average lesser sandhill but not quite as large as the average Canadian sandhill crane. They likely represent one point along the gradation of sandhill cranes from the small, arctic-nesting lessers to the larger greater sandhill cranes of the continental United States and southern Canada, as recently suggested by Tacha (1981). The ECRD population is probably one of the more southerly-nesting of lesser sandhill cranes with breeding areas at latitudes where Canadian sandhills nest. Thus, it would be reasonable to expect them to be larger than most lessers. The smaller means of those cranes measured in California are probably due to the small sample size, or possibly smaller cranes may be moving farther south and wintering in the Merced NWR area. Littlefield (1979) and Drewein and Bizeau (1974) note higher use of more northerly sites by wintering greater sandhill cranes, and more southerly sites by lessers in California and the Central Flyway respectively.

More data are needed to fully assess the subspecific identity of sandhill cranes staging on the ECRD. As suggested for Central Flyway crane populations, where subspecies identification is also difficult (Stephen 1967, Tacha 1981), management of identifiable populations of sandhill cranes may be more practical than management of subspecies populations. Since Pacific Flyway lesser sandhill cranes appear to represent a fairly distinct population, management to maintain their numbers at desired levels would seem feasible.

IV. FOOD HABITS

Sandhill cranes are omnivorous and opportunistic feeders, taking a variety of food items from insects, small mammals, young birds and eggs, frogs, toads, lizards, and other animal matter to cultivated grains, roots and tubers, tender plant shoots, acorns, and berries (Walkinshaw 1949, Harvey et al. 1968, Guthery 1975, Littlefield 1976, Boise 1977, Mullins and Bizeau 1978, Guthery and Lewis 1979, Reinecke and Krapu 1979). The birds generally obtain food solely with the bill but may occasionally scratch with their feet to help uncover food items (Boeker et al. 1961). Like most migratory birds in early fall, cranes must obtain enough food to meet daily requirements, plus continue synthesis of protein for feather growth after molting, replenish body reserves following breeding, and they must store up energy reserves for the upcoming migration (Johnston 1966). Carbohydrates are important in the diet of snow geese during fall to provide a relatively concentrated high-energy food for fat deposition, and to provide calories for protein synthesis (Wypkema and Ankney 1979). Krapu (1981) found that lesser sandhill cranes staging in spring in the Platte River Valley, Nebraska, deposited fat at a daily rate of 13.2 g and 9.2 g for males and females, respectively. In Nebraska, waste corn gleaned by the cranes in harvested cornfields provided the necessary carbohydrate intake to prepare for migration (Reinecke and Krapu 1979).

Since the ECRD is located quite close to crane breeding areas but far from wintering grounds, migrating cranes on the ECRD would be expected to require quantities of high-quality food in fall to prepare for the long flight to wintering areas, but would require lesser amounts in spring when they have already nearly reached their destination. This is reflected in the lower use of the ECRD staging area in spring than in fall. Early spring food items, as indicated by 3 gizzard contents and observations of feeding sites, indicated cranes fed on new graminoid plant shoots along with some insects, mostly beetles (Carabidae). Later in the spring, when flocks of cranes (probably non-breeders), stage on the ECRD for approximately 1 week, bulbs of arrow-grass (*Triglochin palustris*) and tubers of orchids (*Sprianthes romanzoffiana*) were extracted from mossy substrates as soon as the green shoots of these plants emerged.

Fall food items of sandhill cranes are summarized in Tables 7 and 8. Gullet contents of birds are generally a better indicator of food intake than are gizzard contents due to differing breakdown rates of soft and hard foods in the gizzard (Swanson and Bartonek 1970). However, gizzard items were also analyzed in this study due to the greater sample size obtained, the large food volume per gizzard ($\overline{X}$=17.20 ml vs. $\overline{X}$=7.10 ml for gullets), and the fact that most food items in gizzards were identifiable.

Table 7. Food items occurring in 32 sandhill crane gullets during fall 1979 and 1980 on the eastern Copper River Delta, Alaska.

Food item	Frequency of occurrence (%)	Aggregate percentage (%)	Aggregate volume (%)	% of total dry weight
Plant foods				
Triglochin palustris (bulbs)	87.5	73.5	85.1	91.6
[a] *Triglochin palustris* (leaves)	59.4	11.9	5.5	1.6
[a] *Triglochin palustris* (roots)	15.6	1.0	1.5	0.3
Unidentifiable vegetation	9.4	*tr.*	*tr.*	*tr.*
[b] *Carex* spp. (leaves)	6.3	*tr.*	*tr.*	*tr.*
[b] *Potentilla egedii* (leaves)	6.3	*tr.*	*tr.*	*tr.*
Equisetum spp. (leaves)	3.1	*tr.*	*tr.*	*tr.*
Gramineae (roots)	3.1	*tr.*	*tr.*	*tr.*
Ericaceae (fruits)	3.1	*tr.*	*tr.*	*tr.*
[a] Bryophyta (leaves)	3.1	*tr.*	*tr.*	*tr.*
Animal foods				
Gastropoda				
Lymnaeidae (snails)	21.9	5.5	3.3	2.0
Insecta				
Tipulidae (craneflies, adults)	21.9	5.7	2.3	0.6
Tipulidae (craneflies, larvae)	6.3	*tr.*	1.0	2.1
Carabidae (beetles, adults)	3.1	*tr.*	*tr.*	*tr.*
[a] Unknown larva	3.1	*tr.*	*tr.*	*tr.*
Arachnida				
Lycosidae (spiders)	3.1	*tr.*	*tr.*	*tr.*
Grit	18.8	0.5	*tr.*	

[a] Taken incidentally with *T. palustris* bulbs.

[b] Taken incidentally with snails.

tr. (trace) = $\leq$ 0.5 %

Table 8. Food items occurring in 74 sandhill crane gizzards during fall 1979 and 1980 on the eastern Copper River Delta, Alaska.

Food item	Frequency of occurrence (%)	Aggregate percentage (%)	Aggregate volume (%)
Plant foods			
Triglochin palustris (bulbs)	95.2	59.1	64.3
[a]*Triglochin palustris* (leaves)	83.8	18.4	19.4
[a]*Triglochin palustris* (roots)	27.0	5.5	6.3
Unidentifiable vegetation	18.9	10.4	3.2
[a]Bryophyta (leaves)	22.1	*tr.*	*tr.*
Equisetum spp. (leaves and meristems)	4.1	*tr.*	*tr.*
[b]*Carex* spp. (leaves)	2.7	1.5	2.0
Drosera rotundifolia (leaves)	1.4	*tr.*	*tr.*
Animal foods			
Gastropoda			
Physidae (snails)	6.8	0.9	0.8
Insecta			
Tipulidae (craneflies, adults)	28.6	2.6	2.8
Unidentifiable adults	10.4	*tr.*	*tr.*
Odonata (dragonflies, adults)	1.4	*tr.*	*tr.*
Arachnida			
Lycosidae (spiders)	1.4	*tr.*	*tr.*
Hirudinea			
Hirudinidae (leeches)	1.4	*tr.*	*tr.*
Crane feathers	4.1	*tr.*	*tr.*
Grit	100.0		

[a]Taken incidentally with *T. palustris* bulbs.

[b]Taken incidentally with snails.

tr. (trace) = $\leq$ 0.05 %

As clearly shown by both gullet and gizzard contents, the predominant food of most sandhill cranes staging during fall is the bulbs of *Triglochin palustris*, a small grass-like plant of moist habitats. The fibrous roots and leaves of *T. palustris* are also consumed by cranes but are probably incidental, as all leaves and roots found in gullets were attached to bulbs. Thus, when percentage values are combined for *T. palustris* parts, 85-90% of fall-staging sandhill crane diets consist of *Triglochin palustris* as indicated by gullet contents. Bulbs and tubers of various plants have been identified as major natural food items in the diets of cranes in other areas. Harvey et al. (1968) noted the use of corms of sedges (*Carex* sp.) and cottongrass (*Eriophorum* sp.) by cranes on breeding areas and C.M. Boise (pers. comm.) believes cranes eat *Triglochin palustris* bulbs on the Yukon-Kuskokwim Delta, Alaska. Walkinshaw (1949) reports the common use of the bulbs of an unidentified plant as food of cranes wintering on salt flats along the lower Colorado River in Mexico. Corms of nutgrass (*Cyperus* sp.) formed a major portion of the diet of wintering sandhill cranes in southern Texas (Guthery 1975).

Many of the gullets examined from the ECRD were filled with the bulbs of *T. palustris* and little else, indicating the cranes must actively seek out this food source and are adept at extracting the bulbs. One crane had consumed 183 bulbs of this plant at the time of collection. Crane feeding areas were often encountered on

the ECRD in fall, and leftover crane-extracted *T. palustris* plants indicated most cranes pull up the entire plant, then separate the relatively hard bulb from the roots and stem. Individual techniques appeared to differ as some crane gullets contained many entire plants, while others snipped off the leaves and fibrous roots with their bills before swallowing the bulb. A frequent technique simply involved picking the hard inner bulb from the plant, leaving the outer bulb sheaths attached to the uprooted plant.

The method by which the cranes initially located the *T. palustris* plant is unknown. The above-ground portion rarely exceeds 10 cm and most plants have partially senesced by the time most of the cranes arrive in mid-September. Possibly the birds probe in the ground with their bills until they discover a bulb, but more likely they key in on some visual cue. Inspections of crane probe-holes in feeding areas revealed some excess probing, with unsuccessful probes occurring most often at the base of other graminoid plants. In the spring, remains of *T. palustris* in feeding sites did not regularly occur until the new green shoots of the plant had grown above the ground surface. Most *T. palustris* bulbs occurred from 50-80 mm below the surface of the substrate, whether growing in mud or moss. Cranes seemed capable of easily reaching this food source with their bills only, as scratching for bulbs was never observed.

Triglochin palustris is found throughout the ECRD study area and grows in a variety of situations. Dense, pure stands of the

plant occasionally occurred. These were found in muddy or silty substrates near mean high tide line at the edge of the Salt Grass Meadow habitat and along tidal sloughs. These patches at times resembled cultivated lawns due to their high density of *T. palustris*. *T. palustris* was also scattered sparingly throughout the Salt Grass Meadow habitat, occurring most frequently in moist depressions in the mud. The plant was also scattered throughout the Wet Meadow habitat where it grew best in areas where the moss substrate was continually saturated with water or in 3-5 cm of standing water. *T. palustris* grew in substrates composed of the mosses *Rhytidiadelphus squarrosus*, *Sphagnum squarrosum*, *Aulacomnium palustre*, and *Mnium pseudopunctatum*, and was seldom found in drier hummocks and slough banks dominated by *Polytrichum commune*, or shallow ponds where *Drepanocladus uncinatus* formed the major ground cover. Common associated plants included a light cover of *Carex ramenskii*, *C. mackenziei*, *Poa eminens*, *Calamagrostis canadensis*, *Equisetum arvense*, *Potentilla palustris*, and *Epilobium palustre*. Most feeding by staging cranes was done in Wet Meadow habitat, probably due to the soft mossy substrate which made probing and extraction of *Triglochin* much easier than in the dense muddy substrates of Salt Grass Meadows.

Results of nutrient analyses on *T. palustris* bulbs are presented in Table 9. Thomas and Prevett (1980) collected *T. palustris* bulbs from the shores of James Bay and results of their nutrient analyses compare closely to this study. They conclude the bulbs contain

Table 9. Chemical composition (%) of *Triglochin palustris* bulbs on a dry weight basis.

Component	Percent composition of bulbs
Ash	5.3
Crude fat	0.02
Crude protein	14.8
TNC (Total nonstructural carbohydrates)	35.6
P	0.39
K	1.70
Ca	0.60
Mg	0.17

potentially 93-95% digestible nutrients. They were concerned with goose nutrition and digestion capabilities which probably differ somewhat from those of cranes. The percent total nonstructural carbohydrates (%TNC) value in Table 9 probably estimates the digestible carbohydrate values for cranes. Protein levels also are quite high, being higher than those of corn (*Zea mays*) which averages 8.8-10.0% (Nat. Acad. Sci. 1971). Waste corn is a common winter food of cranes and one they often consume before spring migration flights (Reinecke and Krapu 1979). Thomas and Prevett (1980) conclude *T. palustris* bulbs are a high quality pre-migratory food for geese, providing abundant carbohydrates for energy during cooling temperatures and fat deposition in preparation for migration, along with protein for continued growth and build-up of muscle tissue. The same can probably be stated for sandhill cranes which likely utilize these nutrients in a similar fashion. *Triglochin palustris* bulbs are also one of the most important pre-migratory foods utilized by dusky Canada geese staging in the Wet Meadow habitat of the ECRD (Hawkings in prep.). Due to their easy extraction and abundance, *T. palustris* bulbs are likely the best pre-migratory food available on the ECRD to staging sandhill cranes.

Other vegetable foods consumed by cranes were in very low quantities in fall specimens and are relatively unimportant in the diet of staging cranes. Animal foods were also in low quantities, but due to their high protein content they likely provide cranes

with certain essential amino acids, otherwise present only in low quantities in *T. palustris* bulbs (Thomas and Prevett 1980). The major animal foods consumed are snails (family Lymnaeidae) and adult craneflies (Tipula sp.). The snail fraction in gizzards is probably inordinately small due to high digestion rates of the soft body parts, and reduction of the shell to unidentifiable grit-like particles in the gizzard. These invertebrates are likely taken by cranes while searching for *T. palustris* bulbs, as they often occurred in small numbers with bulbs of this plant in gullet samples. A few gullets samples, however, contained almost pure snails or craneflies, indicating cranes specifically seek out these prey items at times. Vertebrates were absent in food samples of cranes taken on the ECRD in 1979 and 1980. In certain years, western toads (*Bufo boreas*) and tundra voles (*Microtus oeconomus*) are abundant on the study area. During 1981 when vole populations were high, staging cranes were observed capturing and eating tundra voles on several occasions. Cranes usually dismembered voles by shaking them vigorously before swallowing them in the manner described by Walkinshaw (1949). The only crane collected in 1981 contained the remains of a tundra vole and a few *T. palustris* bulbs in its gizzard.

The low occurrence of grit in gullet samples indicates they rarely obtain this while feeding in the wet meadow. Occasionally small flocks were observed flying west toward the Copper River in fall, presumably to obtain gravel. Crane gizzards contained an average of 9.78 ml of grit.

Competition for food resources could become important to cranes on the ECRD during prolonged bad weather conditions. Dusky Canada geese also stage in substantial numbers on the ECRD in fall and will also selectively feed on *T. palustris* bulbs, though a wider range of plant foods is available to them than to cranes. Cranes may have difficulty finding *T. palustris* bulbs where geese have fed previously. Wet meadow feeding sites where shrub and grass densities were lowest were favored by both geese and cranes. Few of these areas lacked goose sign by early October. Competition is probably minor at present due to the short staging period of cranes in most years and their relatively early fall arrival on the ECRD. As shrub densities increase in the wet meadow habitat, however, geese and cranes will be forced to feed in a more restricted area and competition for food may increase.

Brown bears were indirectly observed feeding on *T. palustris* bulbs in September and October. Numerous scats were found heavily laced with the undigested bulbs and bulb portions. Patches of torn-up moss over 10 m in diameter were occasionally found where bears had overturned the moss layer to obtain *T. palustris* bulbs. Competition is probably insignificant, however, due to the low density of resident brown bears.

Staging sandhill cranes contained high amounts of body cavity and subcutaneous fat deposits in fall. Abundant fat reserves were found along the intestines, gizzard, heart, and peritoneum of most

cranes necropsied for food habits or parasite loads. An adult male collected 2 September 1980 had 28gm of body cavity fat. Total fat content of cranes could not be measured due to a lack of proper facilities in the field. Krapu (1981) examined carcasses of adult lesser sandhill cranes departing spring staging areas in Nebraska and found they contained an average of approximately 900g and 800g of fat for males and females, respectively. Cranes spending several days on the ECRD in fall likely deposited some fat. Most birds fed almost continually during daylight hours on a relatively rich diet of *T. palustris* bulbs. The addition of fat reserves may have been a primary reason for higher staging activity in 1979. However, the low use of the ECRD in 1980 and 1981 indicates that at least in some years, cranes have deposited adequate fat reserves before passing through the ECRD. Carcasses of several juveniles in 1979 contained few fat reserves, indicating some young birds may be stressed during the long fall flight.

While crane chicks are capable of feeding themselves virtually from the time of hatching, the parent birds will often find food and present it to chicks during daily foraging (Walkinshaw 1949). Frequency of feeding of chicks by adults appeared to decrease over the brood-rearing period on the Yukon-Kuskokwim Delta, but parents were still giving chicks occasional food items in late August (Boise 1977). I commonly observed adult cranes pulling up *T. palustris* bulbs and feeding them to juveniles, although juveniles

were also observed feeding on this plant themselves. On 3 occasions in 1981, adult cranes (presumably the parents) were observed being chased by a juvenile after having captured a tundra vole. They eventually relinquished the prey item to the juvenile. Feeding of juveniles even occurred, though rarely, on wintering grounds at Merced NWR during January and February, when juveniles appeared almost identical to adults.

V. HABITAT USE

Sandhill cranes, while nesting in wetland habitats, often utilize upland meadows and cultivated fields at other times of the year (Walkinshaw 1949, Lewis 1974). For roosting, migratory flocks usually choose sites with level terrain, shallow water, and often exposed mud or sand flats surrounded by water (Lewis 1976, Lovvorn and Kirkpatrick 1981). In all cases, however, sandhill crane habitat consists of level areas of low vegetation where cranes have good visibility, presumably to watch for predators.

I identified 4 major habitat types important to cranes on the ECRD following the classification scheme of Kessel (1979*a*) (Fig. 11). These types are: 1. Medium Shrub, 2. Wet Meadow, 3. Salt Grass Meadow and, 4. Intertidal Mudflat. The most inland type, Medium Shrub, consisted of dense stands of sweet gale (*Myrica gale*), *Carex lyngbyaei*, *Potentilla palustris*, and *Calamagrostis canadensis*, often in standing water 0.5 m deep, or less. Stringers of alder and Sitka spruce occur along the numerous stream banks and lake margins. Large shallow lakes (>20 ha) are frequent throughout the habitat, which extends into the Martin River Valley and eastward to the Ragged Mountains. This habitat comprises approximately 85 km^2 on the ECRD, south of the Martin River.

The Wet Meadow type represents approximately 75 km^2 of former intertidal salt marsh, now a freshwater marsh due to uplift from

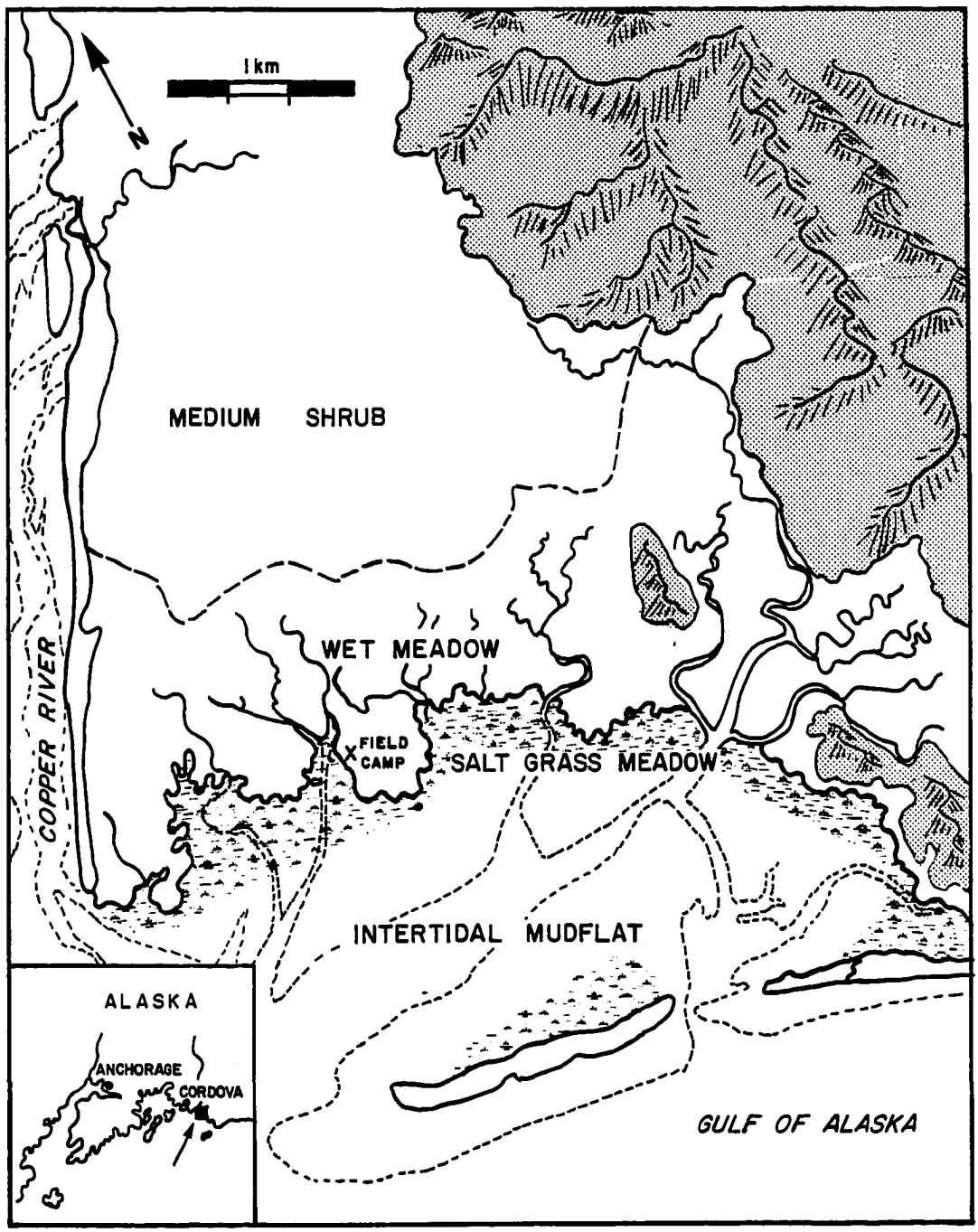

Figure 11. Map of major habitat types on the eastern Copper River Delta.

the 1964 Earthquake. Spruce, sweet gale, alder, and willow scrub has invaded the former salt marsh where woody plant growth had been absent prior to the Earthquake. Vegetation in this area before the earthquake is poorly known for the ECRD, but likely consisted of forb and graminoid communities tolerant of saltwater flooding a few times per year during storm tides or extremely high spring tides (Hawkings in prep.). The freshwater regime after the earthquake permitted a thick blanket of mosses to cover the moist silt and mud substrates throughout the Wet Meadow. To a degree, the moss crowded out other plants, especially on well-drained slough banks, but could not colonize the numerous shallow ponds. Appendix III gives a list of plant species ranked in order of decreasing abundance by percent cover in the Wet Meadow as determined by systematic vegetation plots sampled in this habitat type. Frequency of occurrence of each species in the plots, showing how widespread plants are, is also presented. The 7 highest values by percent cover are all moss species, indicating the predominance of moss as a ground cover. Graminoids are likely underestimated by percent cover values due to their vertical growth forms, but they are the dominant higher plant forms on the ECRD.

The Wet Meadow is a mosaic of plant communities intergrading along the gentle slope from higher, well-drained slough banks to wet depressions and small ponds. East-west and north-south gradients of plant communities also exist, possibly due to substrate and

drainage differences, and seed sources. The mosses *Aulacomnium palustre* and *Mnium pseudopunctatum*, along with *Equisetum* spp. are common in plant communities near Cottonwood Point but are virtually absent near the Spruce Islands where the mosses *Polytrichum commune* and *Sphagnum squarrosum* dominate and Sitka spruce seedlings are abundant. *Potentilla egedii* is common over much of the Wet Meadow and onto the Salt Grass Meadow habitat, but gradually becomes rarer near the Medium Shrub habitat where *P. palustris* dominates. Fig. 12 illustrates a typical view of Wet Meadow vegetation near the 1979, 1980 camp site.

The Salt Grass Meadow consists of 10 km^2 of former intertidal mudflats that became vegetated following uplift by the 1964 Earthquake. Halophytic plants such as *Carex ramenskii*, *Plantago maritima*, *Potentilla egedii*, and *Puccinellia* spp. have invaded to mean high tide line over most intertidal mudflats. Moss cover (*Psilopilum laevigatum* and *Dicranella* sp.) is present along the Wet Meadow fringe where only storm tides now reach. Varying amounts of the Salt Grass Meadow are covered at each high tide, with storm tides or very high spring tides covering virtually all of this habitat. Plant diversity and abundance decreases from the Wet Meadow edge toward mean high tide line, where only *Puccinellia* spp. are able to grow. Woody vegetation is absent from this habitat and substrates consist of bare mud and silt. A typical view of the Salt Grass Meadow is shown in Fig. 13. Plant species found on systematic

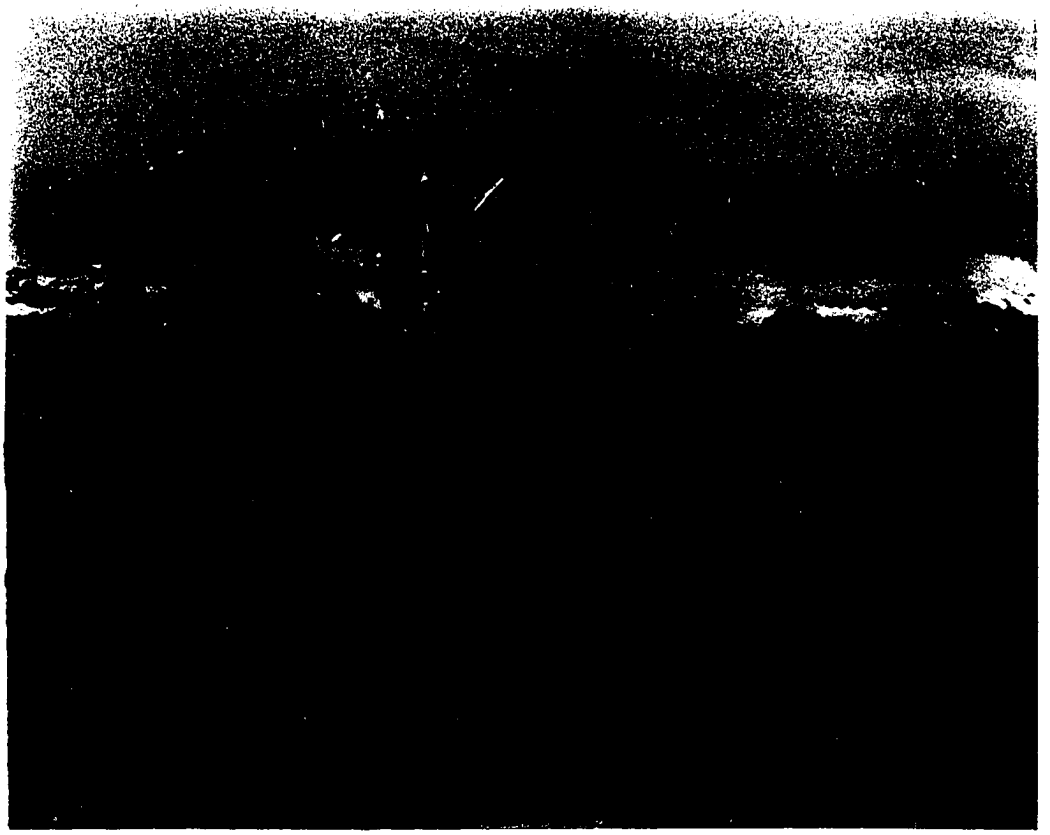

Figure 12. View of typical Wet Meadow vegetation on the eastern Copper River Delta.

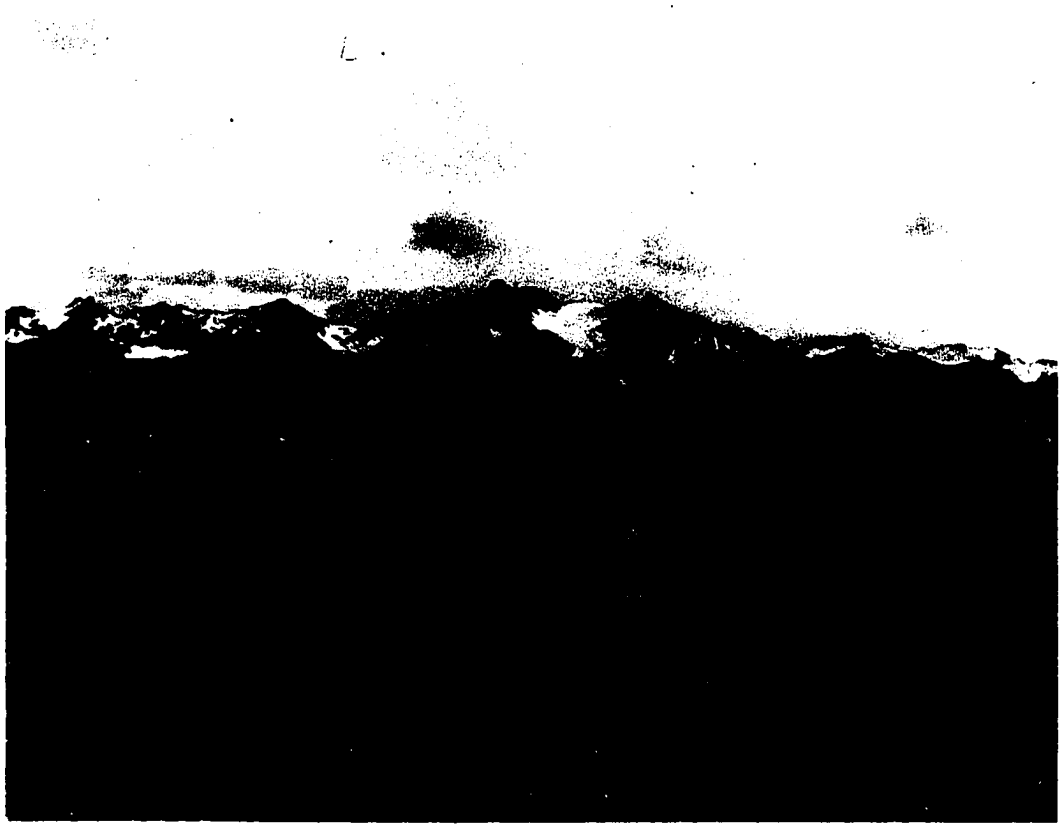

Figure 13. View of typical Salt Grass Meadow vegetation on the eastern Copper River Delta.

vegetation plots taken across this habitat are presented in Appendix IV. A list of plants identified on the ECRD but not found on vegetation plots is presented in Appendix V.

The Intertidal Mudflat habitat is covered by tides twice daily and is unvegetated except for a sparse growth of macroalgae (*Ulva* sp.). The 65 km^2 expanse of open mudflats is broken only by the brackish sloughs which drain all 4 habitat types.

A. Feeding Habitat

Observations from the tower and tree platforms indicated staging cranes fed almost exclusively in the Wet Meadow habitat type. Figs. 14-17 indicate the degree of crane use on the ECRD as noted during daylight hours from the main camp in 1979 and 1980. Only local flights, generally to and from feeding or loafing sites, were included in the figures. Evening flights to roosts were not included. Less use of the ECRD for staging in spring, as mentioned in Section I, is further revealed by the smaller circles on spring habitat use maps (Figs. 14,15). Major use areas in both fall 1979 and 1980 were near the boundary of Medium Shrub habitat, and just west of the Spruce Islands. Local commercial fishermen and hunters have long noted the use of areas between the Copper River Dunes and Russian River Slough by staging cranes (D. Curran, R. Gill, and M.E. Islieb pers. comm.). In recent years, even over the course of

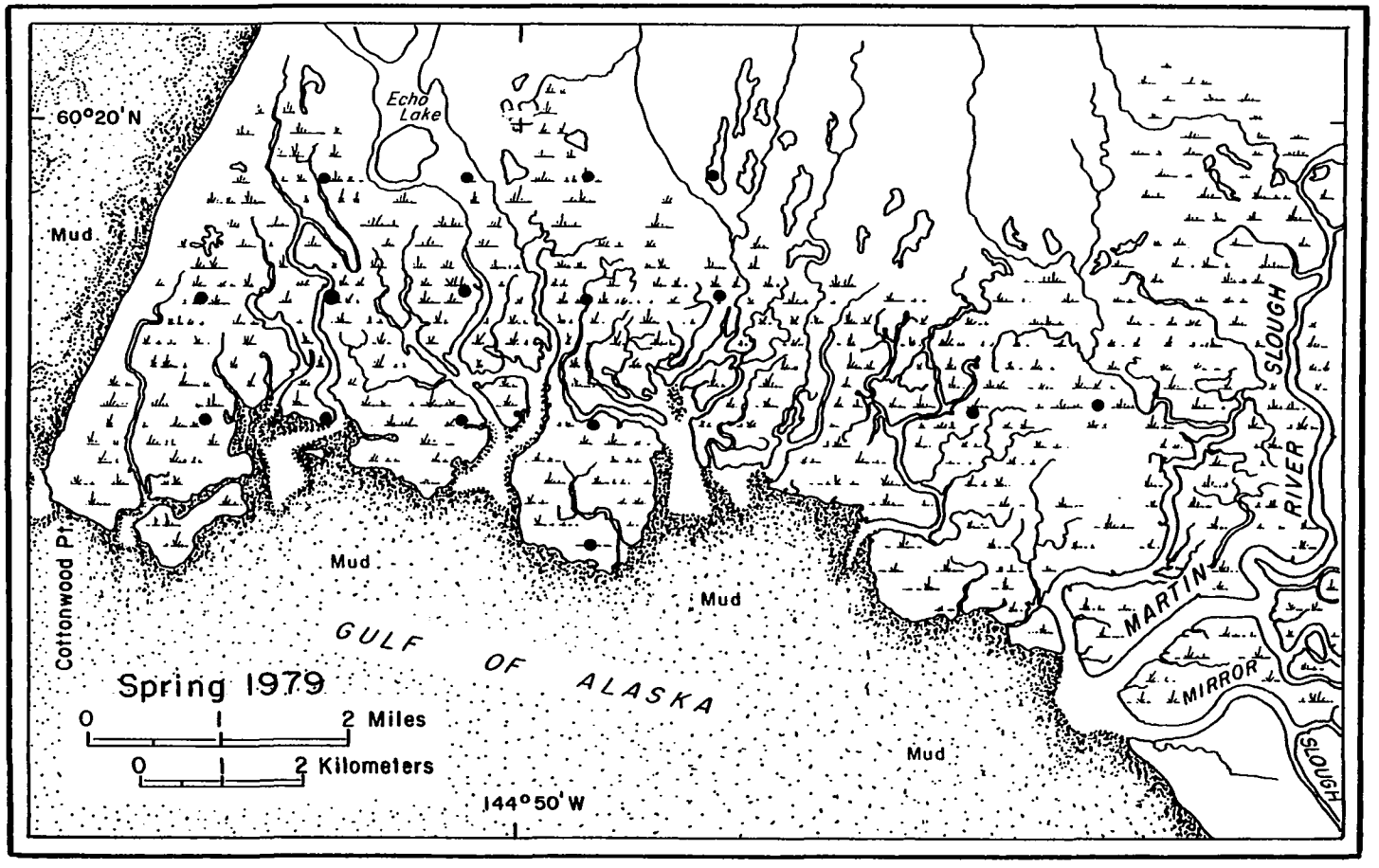

Figure 14. Sandhill crane use areas on the eastern Copper River Delta in spring 1979. Larger sphere indicates greater use per survey section (2.56 km^2). Each millimeter of sphere diameter represents 500 cranes observed landing in that section.

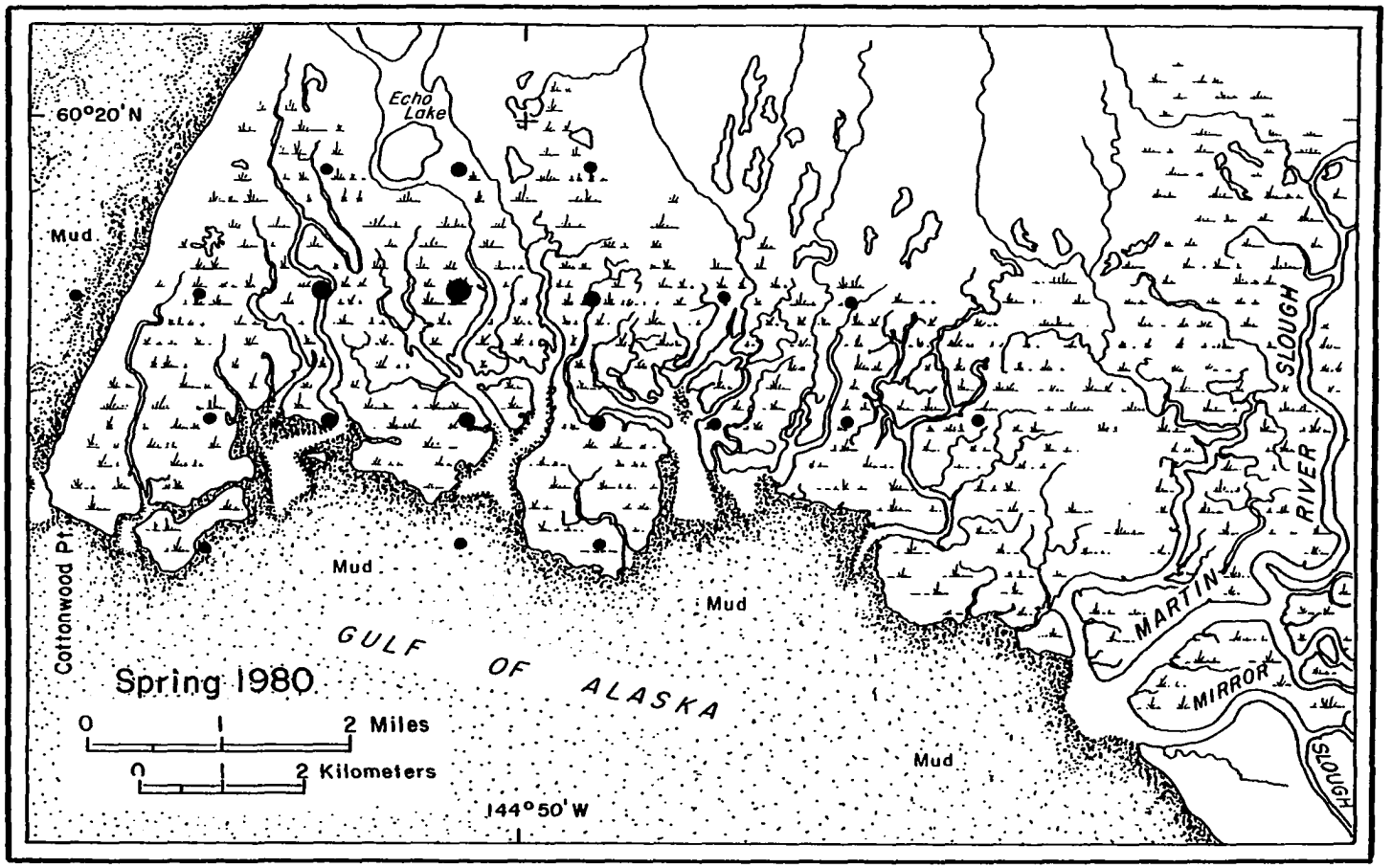

Figure 15. Sandhill crane use areas on the eastern Copper River Delta in spring 1980. Larger sphere indicates greater use per survey section (2.56 km^2).

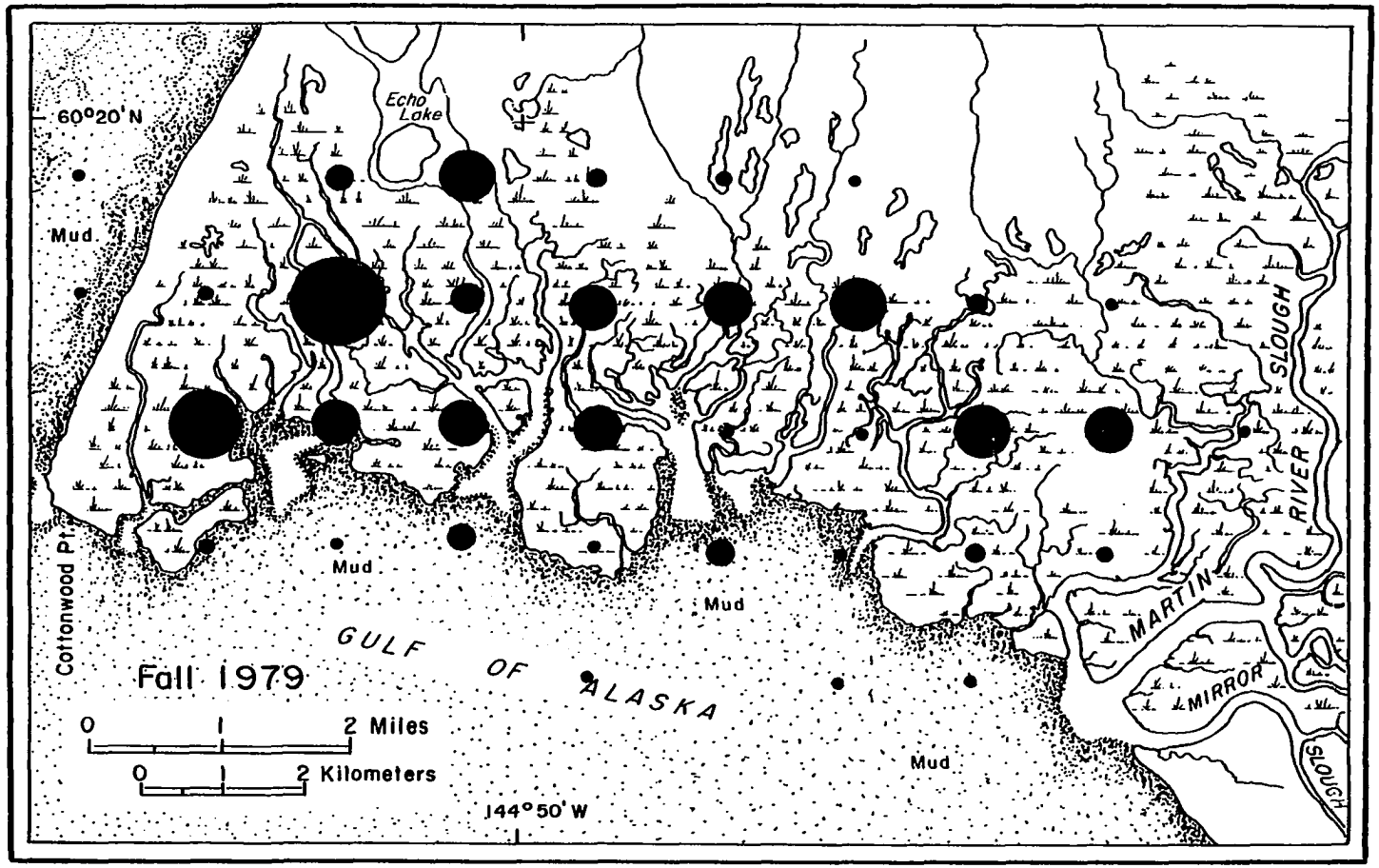

Figure 16. Sandhill crane use areas on the eastern Copper River Delta in fall 1979. Larger sphere indicates greater use per survey section (2.56 km^2).

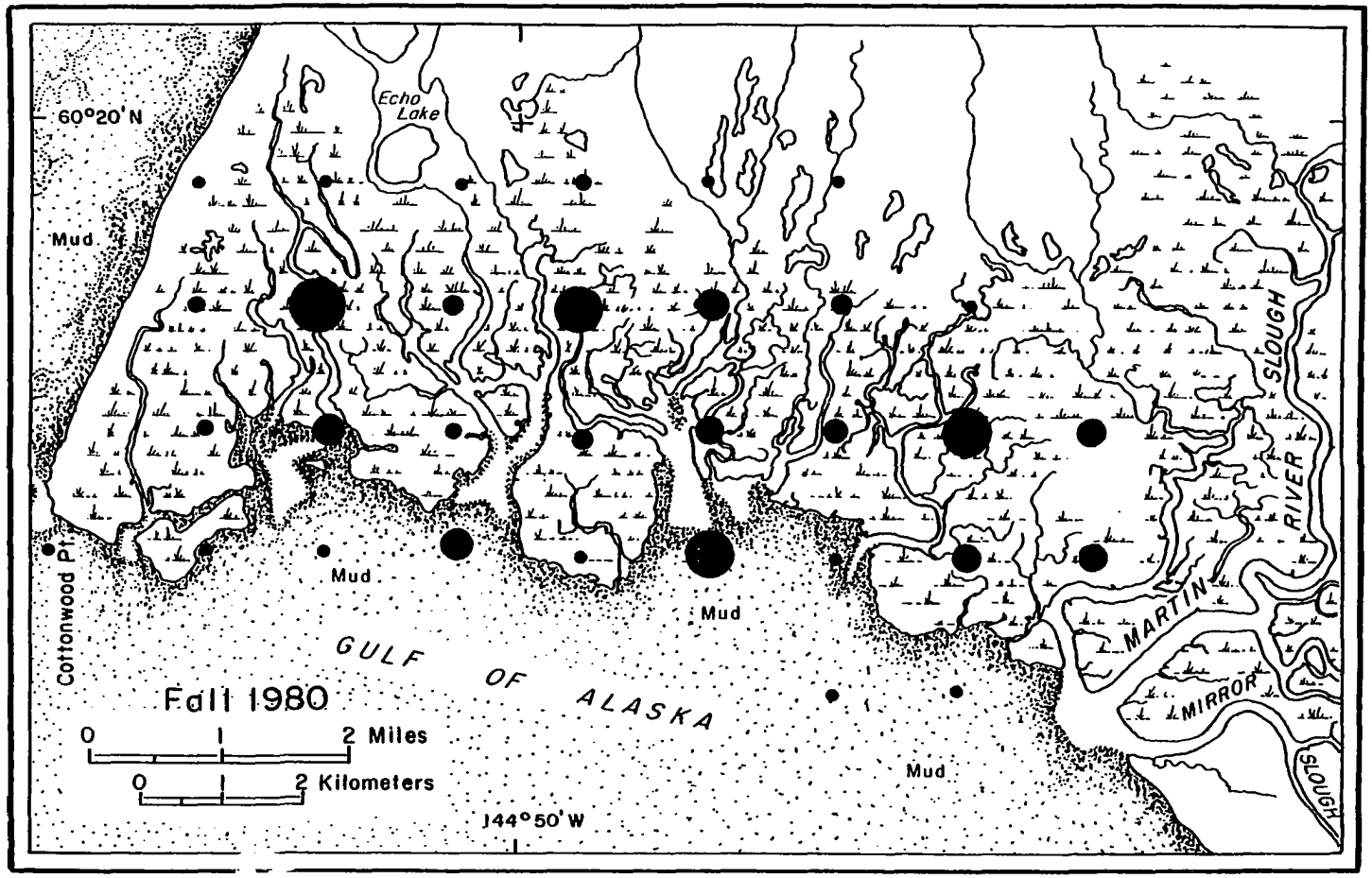

Figure 17. Sandhill crane use areas on the eastern Copper River Delta in fall 1980. Larger sphere indicates greater use per survey section (2.56 km^2).

the present study, increased use of more eastern areas near the Spruce Islands has occurred. Shrub expansion since the 1964 Earthquake, resulting in closure of openings in the more well-drained Russian River Slough area, is apparently forcing cranes farther east where large openings still exist. Cranes could rarely be seen east of the Spruce Islands from the camp site in 1979 and 1980, but observations from the Spruce Islands in 1981 indicated only light use of this area. Cranes only rarely fed in the Salt Grass Meadow. This habitat was occasionally used for secondary roosts (an area where cranes preened, danced, and rested immediately preceding or following nighttime roosting (Wheeler and Lewis 1972), or as a refuge area from hunter or aircraft harassment. A flock of 63 cranes was observed actively feeding on *T. palustris* in this habitat on 8 September 1980. No indication of feeding in Medium Shrub or Intertidal Mudflat habitats was observed.

Feeding habitat was further defined by principal components analysis (Davis 1973). Comparison of feeding plots along the second and third components explaining the highest amount of variability among the systematic vegetation plots, revealed some separation of feeding plots into a subgroup (Fig. 18). Component 2 explained 17.4% of variability and represented substrate moisture. Plants preferring wet sites (*Drepanocladus uncinatus, Mnium pseudopunctatum, Carex lyngbyaei*) had low negative loadings onto component 2, and plants preferring well-drained locations (*Alnus sinuata,*

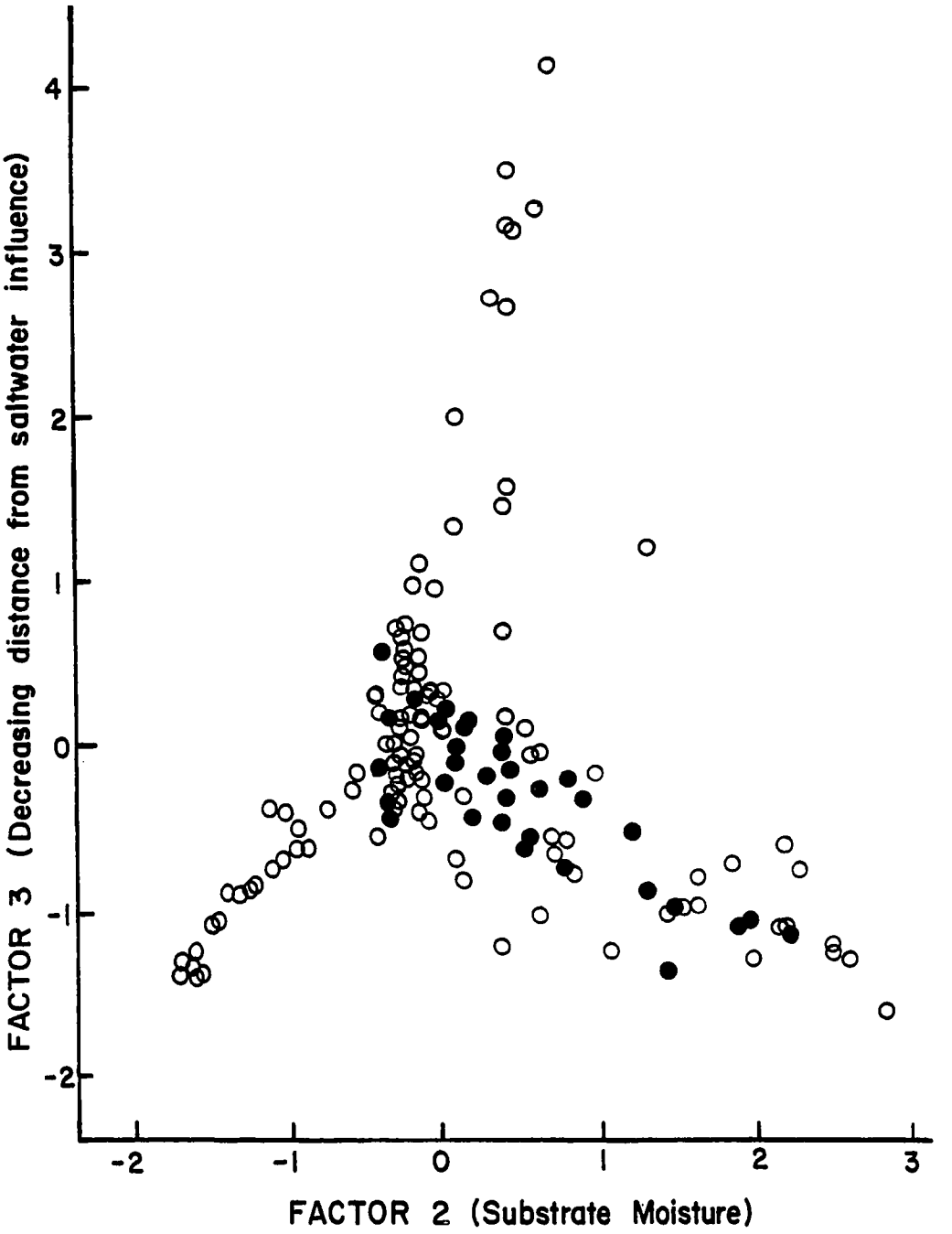

Figure 18. Feeding site selection of staging sandhill cranes as determined by principal components analysis of systematic vegetation plots (open circles) and vegetation plots taken at feeding sites (closed circles).

Equisetum spp.) had high positive values. Component 3 explained 13.4% of variability and represented position along the south-north gradient across the wet meadow, reflecting decreasing distance from saltwater influence. Plants typical of sites near the Wet Meadow-Medium Shrub interface (*Drepanocladus uncinatus, Myrica gale*) scored low negative loading values onto component 3, while plants found commonly at the Wet Meadow-Salt Grass Meadow interface (*Psilopilum laevigatum* and *Dicranella* sp., *Alnus sinuata, Deschampsia caespitosa*) had high positive values. Location along component 3 of plots taken near these interfaces further substantiated interpretation of this component.

Positions of plots taken at feeding sites in Fig. 18 along the lower right leg of the figure indicated cranes chose areas of moist to fairly dry substrates nearer the Wet Meadow-Medium Shrub interface. Avoidance of areas near the Wet Meadow-Salt Grass Meadow border probably results from preference for open sites, uncommon at this interface where a dense stand of alders predominates. Avoidance of very wet feeding sites is probably due to a lack of *Triglochin palustris* there. A typical feeding area of cranes on the ECRD seems to consist of an open site of moist to fairly dry substrates, and occurs more commonly farther north in the Wet Meadow.

The major food plant of cranes on the ECRD, *T. palustris*, superficially resembles a small sedge or grass and is scattered throughout graminoid communities. Cranes likely keyed-in on associated

plants to identify communities where *T. palustris* was growing. A Kolmogorov-Smirnov goodness of fit test (Zar 1974) was applied to frequency distributions of percent occurrence values from vegetation plots. Comparisons of cumulative distributions of plant species percent cover between the systematic plots and plots at feeding sites by this test revealed plants most indicative of feeding sites. Plant species scoring highly positive D-values (Table 10) represent species more common at feeding sites than expected, based on the systematically taken vegetation plots. Highly negative D-values indicate species rarely found at feeding sites. Although only 5 species were significantly different ($p \leq 0.05$) from expected distributions, all common plants are listed to illustrate the trend of species representation at feeding sites. Generally, cranes chose sites dominated by the sedge *Carex ramenskii*, along with a light cover of the grasses *Poa eminens*, *Calamagrostis* spp., and *Agrostis* spp. Substrates at crane feeding sites usually consisted of 100% moss cover, with *Rhytidiadelphus squarrosus*, *Aulacomnium palustre*, *Mnium pseudopunctatum*, and *Sphagnum squarrosum* being common forms. The low D-values of the two common shrubs, alder and upright or bush-form willows, further identify preference for open, brush-free habitat. Crane avoidance of wet sites is shown by the low values for *Carex lyngbyaei* and the moss *Drepanocludus uncinatus*. Several plant species, such as *Parnassia palustris*, *Spiranthes romanzoffiana*, and *Rhinanthus minor* had senesced considerably by

Table 10. Results of Kolmogorov-Smirnov goodness of fit test on vegetation plots (a indicates significant deviation from expected distribution based on systematically-taken vegetation plots).

Plant species	$D_{\alpha=0.05}$
Carex ramenskii	+0.814[a]
Rhytidiadelphus squarrosus	+0.538[a]
Aulacomnium palustre	+0.259
Poa eminens	+0.258
Calamagrostis spp.	+0.247
Mnium pseudopunctatum	+0.239
Sphagnum squarrosum	+0.234
Agrostis spp.	+0.221
Stellaria spp.	+0.168
Dwarf *Salix* spp.	+0.167
Potentilla palustris	+0.134
Carex mackenziei	+0.122
Deschampsia beringensis	+0.116
Juncus alpinus	+0.097
Triglochin maritima	+0.093
Helodium blandowii	+0.089
Eleocharis kamtschatica	+0.059
Carex pluriflora	+0.021
Triglochin palustris	+0.021

Table 10. (cont.)

Lomatagonium rotatum	-0.003
Deschampsia caespitosa	-0.025
Galium trifidum	-0.030
Agrostis exarata	-0.031
Peltigera sp.	-0.031
Plantago maritima	-0.054
Primula egaliksensis	-0.064
Ranunculus cymbalaria	-0.081
Rumex fenestratus	-0.085
Euphrasia mollis	-0.101
Eriophorum scheuchzeri	-0.104
Polytrichum commune	-0.106
Epilobium adenocaulon	-0.109
Psilopilum laevigatum and *Decranella* sp.	-0.124
Myrica gale	-0.142
Epilobium hornemannii/palustre	-0.165
Equisetum spp.	-0.168
Chrysanthemum arcticum	-0.176
Upright *Salix* spp.	-0.179
Alnus sinuata	-0.192
Parnassia palustris	-0.210
Carex lyngbyaei	-0.247

Table 10. (cont.)

Potentilla egedii	-0.261
Spiranthes romanzoffiana	-0.264[a]
Rhinanthus minor	-0.318[a]
Drepanocladus uncinatus	-0.320[a]

September, which likely resulted in unusually low D-values. *Triglochin palustris*, the plant actually sought at feeding sites, was also underrepresented in the analysis as it was difficult to distinguish from sedges while viewing the vegetation plots, and was therefore rarely recorded.

Cranes often fed near Russian River Slough, Echo Lake, the Medium Shrub edge, and near the Spruce Islands in fall. Cranes selected open, brush-free sites with moist to dry substrates, generally in the moss-covered areas between well-drained slough banks and wet depressions and pond edges. Plant communities on these sites were dominated by *Carex ramenskii* and several grasses, with moss substrates of *Rhytidiadelphus*, *Aulacomnium*, *Mnium*, and *Sphagnum* being preferred areas for feeding on *T. palustris*.

Availability of feeding habitat was assessed in 1980 and results are presented in Fig. 19. When compared to feeding areas actually used in Figs. 16 and 17, regions of available habitat (wide bars along transects) correspond closely with areas of high use (large spheres). Since determination of favorable crane habitat was accomplished subjectively based on previous experience of observers at crane feeding sites, results may vary due to personal biases. Observers assessed feeding habitat on the basis of opening size, substrate moisture, plant communities, and indications of feeding by cranes. By extrapolating distances across feeding habitat and total length of all transects, approximately 20% (10 km^2)

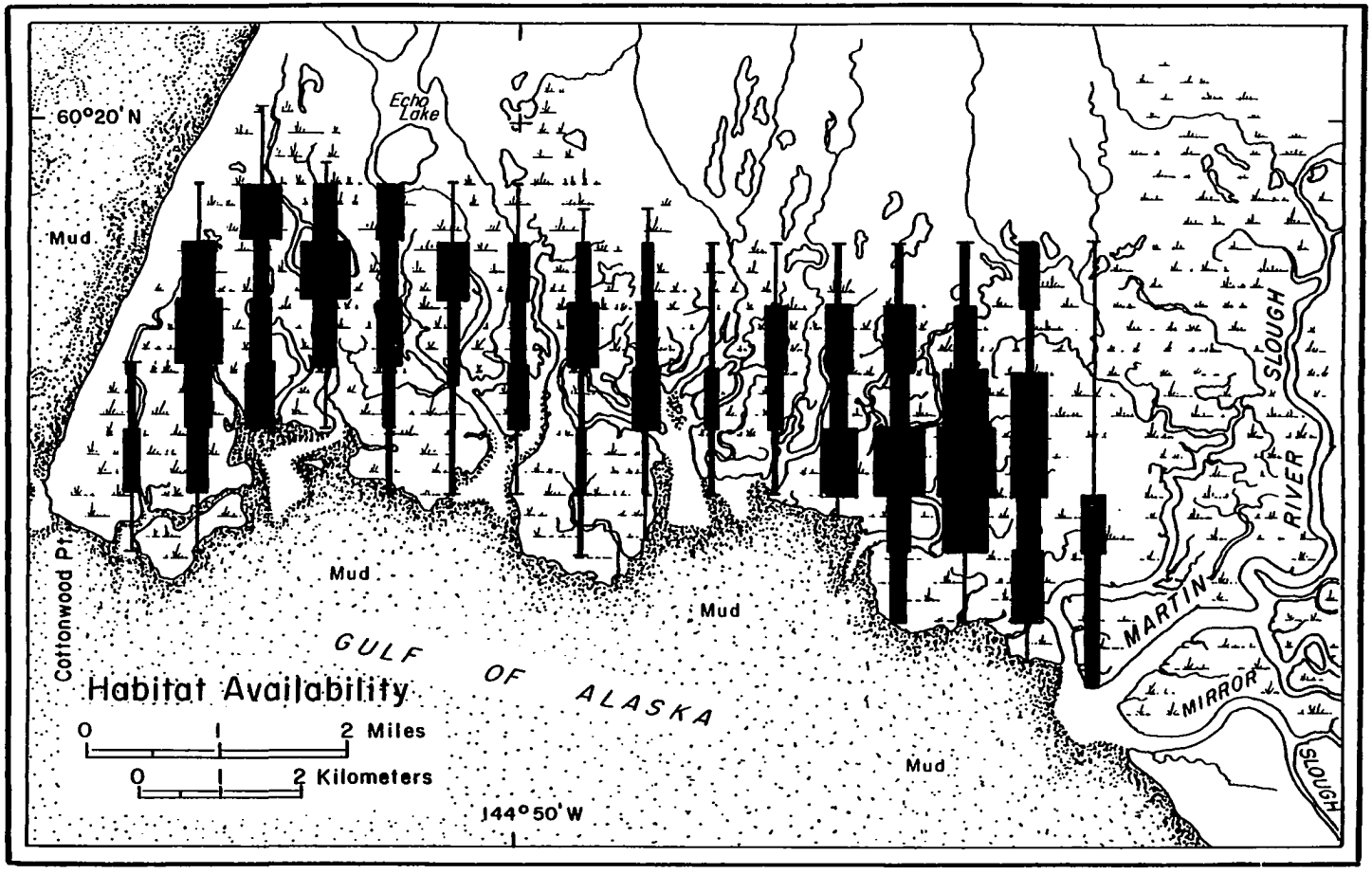

Figure 19. Map of feeding habitat availability transects measured in October 1980. Wider bar indicates greater amount of available feeding habitat per 800 m of transect. Each millimeter of bar width represents 0.1 km of feeding habitat per transect segment (0.8 km).

of the Wet Meadow west of the Spruce Islands was estimated to be favorable crane feeding habitat in 1980.

Shrub encroachment in the Wet Meadow since the 1964 Earthquake may be the greatest threat to present crane habitat on the ECRD. The Salt Grass Meadow will remain open and brush-free due to periodic tidal flooding. Staging cranes may resort to feeding in this habitat more in the future, if the Wet Meadow becomes too closed. *Triglochin palustris* grows in the Salt Grass Meadow but the muddy substrates are relatively dense. Cranes may not be able to extract bulbs at the rate they can in the soft mossy substrates of the Wet Meadow.

B. Roosting and Roost Habitat

Cranes strive to choose roost sites that are inaccessible to predators, isolated from human activity, and close to feeding areas (Lewis 1976). Roost sites in other areas of North America almost always consist of level terrain with standing water 10-20 cm deep and with short and sparse vegetation. These sites often have exposed mudflats or sandbars where cranes land prior to wading into the water to roost (Lewis 1976, Taylor 1976, Lovvorn and Kirkpatrick 1981, Soine in press). If shallow water areas are absent, cranes may occasionally roost on dry land (Lewis 1976). Cranes required open areas of river channels > 50 m wide for roosting along the

Platte River in spring, but preferred areas > 150 m wide (Krapu 1981). Roost sites used by cranes on the ECRD had similar characteristics, although actual sites varied greatly over the fall staging period.

Roosting sandhill cranes used all four major habitat types on the ECRD (Table 11). Preferences by crane flocks to roost in the Medium Shrub habitat was noted in all falls. I could not observe cranes on the ground in the Medium Shrub habitat so actual roost sites there are unknown. Numerous large shallow lakes with sparse sedge, sweet gale, and *Potentilla palustris* cover were noted in this habitat during aerial surveys in 1981, and are likely used by roosting cranes. Cranes flying to roost in the Medium Shrub habitat often landed < 2 km north of the Wet Meadow, where the only open, brush-free sites were these shallow, vegetated lakes. At other times, cranes continued to fly farther north to the vicinity of the Martin River. An 8 km^2 shallow flooded section of the south branch of the Martin River was the only major opening observed in this area during aerial surveys, except for unvegetated river bars within the Martin and Copper Rivers themselves. This area was likely kept open by summer flooding due to increased outflow from upriver glaciers. In fall, this area had numerous exposed gravel flats. Flooded portions contained only shallow water (< 20 cm deep), and appeared to be an ideal crane roost site. Ground observations in the Medium Shrub habitat are needed to further substantiate roosting locations of cranes.

Table 11. Habitat types selected by roosting sandhill cranes during fall on the eastern Copper River Delta.

Habitat type	Number of cranes (%)			
	1979	1980	1981	Total
Medium Shrub	4531 (38)	4251 (62)	3710 (41)	12,542 (45)
Wet Meadow	1733 (15)	1108 (16)	4040 (45)	6881 (25)
Salt Grass Meadow	1584 (13)	345 (5)	100 (1)	2029 (7)
Intertidal Mudflat	4107 (34)	1115 (17)	1200 (13)	6422 (23)
Total	12,005(100)	6819(100)	9050(100)	27,874(100)

Wet Meadow roost sites were also commonly used in fall, and were the only sites used by cranes roosting overnight in spring. Shallow ponds were chosen roost sites in this habitat, although they were seldom <3 ha in size. Except in spring, large flocks of staging cranes rarely chose to roost in the Wet Meadow during fair weather, but were forced to use these sites when heavy rain and winds >30 km/h virtually grounded cranes near their feeding areas.

Intertidal Mudflats were second in importance among habitats actually selected for roosting. Cranes usually landed near the edge of water in the lagoon system behind the barrier islands. Two tide cycles occur over approximately a 24-h period on the CRD. Roosting cranes were usually forced to walk inland with the advancing tide sometime during the night when roosting on Intertidal Mudflats. This was evidenced by flocks of roosting cranes gathered near the Salt Grass Meadow-Intertidal Mudflats interface at sunrise. Flocks of cranes arriving on the ECRD near sunset, often chose to roost on Intertidal Mudflats rather than flying to Medium Shrub roost sites. Occasionally, however, cranes staging for several days still chose to roost on the Intertidal Mudflat habitat. On 23 September 1979 and 5 September 1980, over 2000 and 250 cranes, respectively, flew to roost sites in the Medium Shrub habitat, but after 10-15 min moved *en masse* to Intertidal Mudflat roosts. It appeared as if something had scared them off their roosts in the Medium Shrub habitat, possibly coyotes (*Canis latrans*) or brown bears.

Cranes only infrequently used Salt Grass Meadow roosts, probably due to lack of standing water and the close proximity to thick brush cover at the Wet Meadow interface over much of this habitat. Sites near the mouths of Russian River and Gus Wilson Sloughs were most frequently used by cranes. All flocks roosting in this habitat were < 500 birds in size, smaller than gatherings of roosting cranes in other habitats.

Numbers of days cranes spent roosting in the 4 habitat types tested with chi-square contingency tests, indicated little relationship to tidal stage (high or low) and weather conditions (wind and precipitation). Cranes showed no habitat preferences when tides were high or low (χ^2 = 1.198, df = 3, $p>0.05$), and were observed landing on Intertidal Mudflats at or near high tides on 5 days. Differential roosting habitat selection was not significant during severe (windy and rainy) or fair (partly cloudy to clear, and mild winds) weather (χ^2 = 3.25, df = 3, $p>0.05$) on the ECRD. Trends were observable, however, as cranes seldom chose to roost on Intertidal Mudflat or Salt Grass Meadow sites during very severe storms. These sites are totally unprotected from the strong southeasterly winds off the Gulf of Alaska. As noted earlier, cranes were often forced to remain on Wet Meadow sites during such severe weather. Lewis (1976) also recorded changes in roost sites of cranes in Oklahoma during very severe storms.

Roost sites are often used regularly from year to year and a high tradition of use develops (Lewis 1974). This may play a part in the consistent use of habitats by cranes on the ECRD, regardless of tidal coverage or weather factors.

Sandhill cranes exhibit relatively consistent arrival and departure schedules to and from evening roosts. Bennett (1978) found 15% of cranes left roosts before sunrise in Wisconsin, while 18%, 25%, and 25% had left roosts by sunrise in Oklahoma (Lewis 1974), Florida (Walkinshaw 1949), and Saskatchewan (Stephen 1967), respectively. Cranes on the ECRD, however, left roosts earlier, as 77% left roosts before sunrise during fall 1979-1981 (Fig. 20). Flights to evening roosts on the ECRD showed greater similarity to other studies, as 69% arrived at roosts by sunset in fall 1979-1981 (Fig. 21). In Oklahoma, 56% had arrived by sunset (Lewis 1974), with similar observations made in Texas and Florida (Walkinshaw 1949), and Wisconsin (Bennett 1978). Cranes occasionally arrived at roosts more than 2 h before sunset (Fig. 21). Cloudy weather tended to delay departures from roosts and initiated flights to roosts earlier than on clear days, indicating light levels probably trigger roosting behavior in cranes (also Walkinshaw 1949, Bennett 1978).

Secondary roosting in cranes occurs in the morning immediately following evening roosting, and preceeds evening flights to roosts (Wheeler and Lewis 1972). At these times, cranes rest, preen,

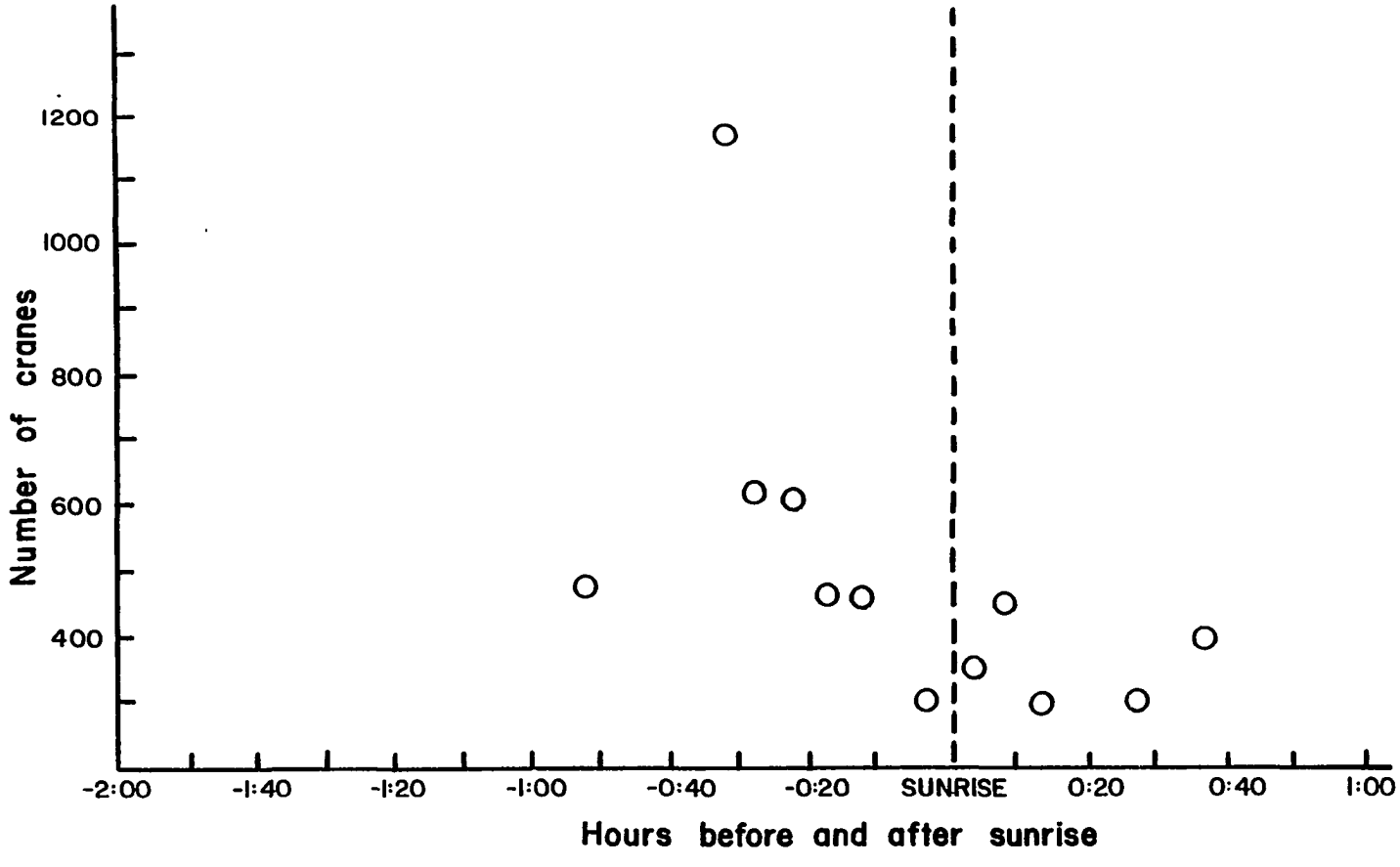

Figure 20. Time of departure of sandhill cranes from roost sites in relation to sunrise during fall 1979-1981.

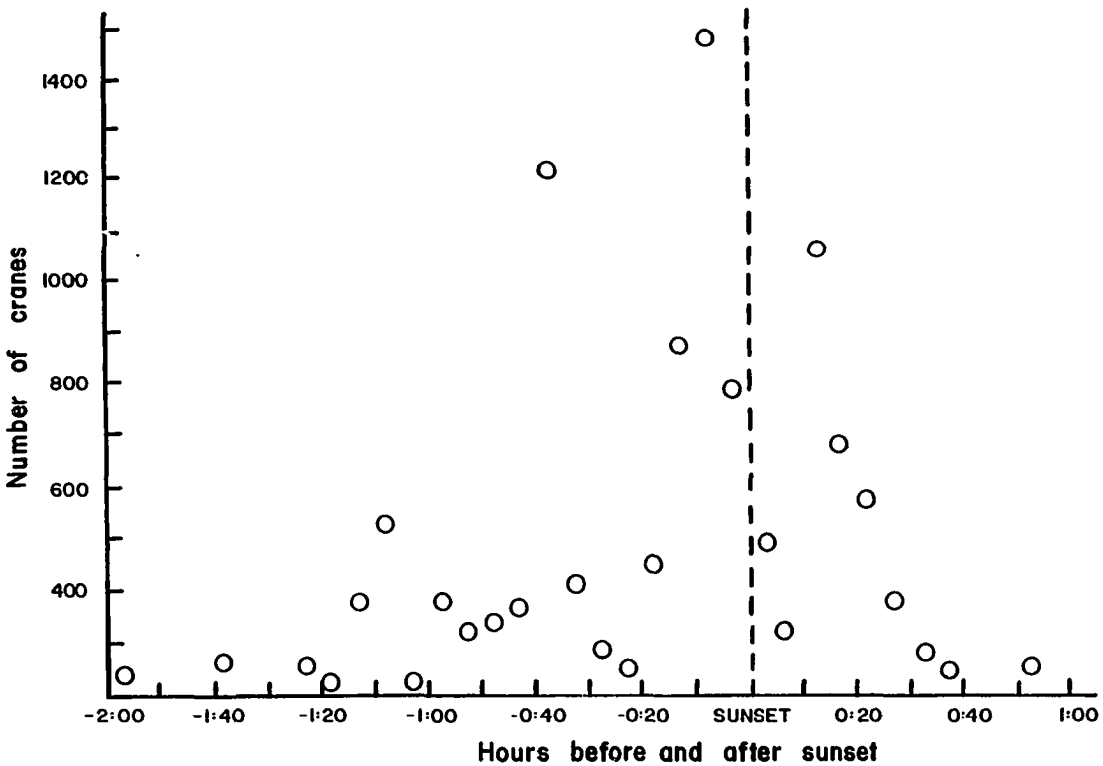

Figure 21. Time of departure of sandhill cranes to roost sites in relation to sunset during fall 1979-1981.

dance, and may do some feeding before flying to feeding areas or roost sites. Similar behavior was occasionally noted on the ECRD. On 8 September 1979, after roosting on Intertidal Mudflats, 200 cranes rested and preened on the wide Salt Grass Meadow banks of Little River Slough for 15 min before flying to Wet Meadow feeding areas. Cranes often gathered in large meadows near Echo Lake for 15-30 min before flying to Medium Shrub roost sites in fall. Use of secondary roosts was not consistent, however, as cranes often flew directly between feeding areas and evening roost sites. Preening and other behaviors performed at secondary roosts may still have been enacted at feeding or roosting areas, however.

The remote roost sites of cranes on the ECRD appear to be safe from human disturbance and habitat destruction threats at present. The dynamic natural forces of glacial flooding and ocean tides which maintain roost habitat, also precludes human interference to a large degree.

VI. AGE AND SEX RATIOS

A. Age Ratios

Tallies of age ratios on lesser sandhill crane flocks can be accomplished with good reliability only through October, when juveniles are still sufficiently different from adults (Lewis 1974). Table 12 presents the results of age ratio counts made on the ECRD study area during the fall staging periods of 1979, 1980, and 1981. In 1979 and 1980, the overall recruitment rate was approximately 7%, but totalled approximately 11% in 1981. Studies of age ratios of Canadian and lesser sandhill cranes in the Central Flyway have been summarized by Buller (1976), these age ratios center around an 11% recruitment rate. Age ratios of lesser sandhills have not been systematically tallied in other areas of the Pacific Flyway. Comparisons of age ratios gathered during the 3 15-day periods of the fall staging period were accomplished using a one-way analysis of variance and arcsine transformation, (Zar 1974). Newman-Keuls test ($p \leq 0.05$) was subsequently applied to the 1980 and 1981 data to detect significance between percentages. Proportions of juveniles did not vary significantly ($F = 0.002$, $df = 2/1589$) through the 1979 staging period, but did between subsequent 15-day periods of 1980 ($q = 32.54, 36.74$; $p = 2, 2$; $DF = 57$) where the proportion of juveniles increased steadily through the fall. In

Table 12. Sandhill crane age ratio counts taken in fall on the eastern Copper River Delta, Alaska.

Time period	Number of cranes	Number of juveniles	Percent juveniles
1979			
24 Aug - 7 Sep	595	39	6.55
8 Sep - 22 Sep	479	31	6.47
23 Sep - 7 Oct	518	34	6.56
Total 1979	1592	104	6.53
1980			
24 Aug - 7 Sep	870	39	4.48
8 Sep - 22 Sep	1003	82	8.18
23 Sep - 7 Oct	235	32	13.62
Total 1980	2108	153	7.25
1981			
24 Aug - 7 Sep	76	8	10.53
8 Sep - 22 Sep	2241	237	10.58
23 Sep - 7 Oct	278	51	18.35
Total 1981	2595	296	11.40

1981, the third period (late September) had a significantly higher ratio ($q = 14.88, 2153$; $p = 2.2$; $DF = 96$) than the earlier periods. Miller and Hatfield (1974) and Buller (1976) also noted an increase in proportion of young cranes as the fall migration progressed in the Central Flyway. As they suggest, the earlier migrants are likely non-breeders, with the majority of family groups migrating later, a situation also noted among geese (Cooch 1958). It is interesting, however, that this pattern failed to occur in 1979 on the ECRD. Migration of cranes in 1979 was somewhat later than in 1980 or 1981, and family groups may have been able to migrate with earlier non-breeders.

The overall productivity of 7% young in 1979 and 1980 was low in comparison to the Central Flyway figure of 11%. Possibly the survey years of 1979 and 1980 represented particularly poor breeding conditions on the as yet undetermined breeding areas of this population of lesser sandhills. The fact that the 1981 age ratio equalled the Central Flyway average seems to indicate this population can be as productive as the Central Flyway birds.

Hunting parties on the study area were actively sought in 1979 to obtain food habits information. Of 46 harvested cranes inspected, 10 were juveniles, providing a sample productivity of 21.74% young. Compared to the approximate 7% young consistently observed in staging flocks throughout 1979, this may indicate a higher susceptibility of juvenile cranes to hunting pressure. Some hunters inter-

viewed, however, showed a preference for bagging the tender young birds over older, tougher cranes which would tend to inflate the number of young in hunters' bags. Juveniles also constituted a higher percent (15-20%) in hunters' bags in the Central Flyway than generally observed in feeding crane flocks (Buller 1976).

As noted by Miller and Hatfield (1974), family groups of cranes tended to feed alone on fall staging areas in Saskatchewan. Therefore, counts of juveniles in large feeding flocks were biased against juveniles. As shown in Table 13, I also found larger flocks (>50 birds) contained fewer juveniles. In all years, percent juveniles in small flocks (<10 birds) were significantly higher ($p < 0.05$) than in large flocks. All flock sizes were included in calculations of age ratios to avoid bias in either direction.

Since age ratios were often tallied on sizeable feeding or resting flocks or flying flocks, family sizes were often difficult to determine. Family size information obtained is presented in Table 14. The 14.3% figure for 2-chick families is comparable to other sandhill crane populations (Buller 1976, Littlefield 1976, Boise 1981), and yields an average family size of 1.2 young. The 3-chick brood observed on 26 August 1980 is unusual for sandhill cranes. Of 137 nests of lesser sandhill cranes studied on the Yukon-Kuskokwim Delta, only 1 contained 3 eggs (Boise 1981). R. Drewein (pers. comm.) and C. Littlefield (pers. comm.) have observed 3-chick broods of greater sandhill cranes. Miller (1973) suggests

Table 13. Percent of juveniles in large (≥ 50 birds) and small (≤ 10 birds) flocks of staging sandhill cranes (n=number of birds).

Year	Large flocks	Small flocks
	% juveniles(n)	% juveniles(n)
1979	4.71 (870)	23.47 (98)
1980	5.49 (983)	15.94 (69)
1981	8.76 (1712)	21.40 (271)

Table 14. Sandhill crane family sizes observed during fall on the eastern Copper River Delta (percent of totals in parentheses).

Year	Number of families with:			
	1 juvenile	2 juveniles	3 juveniles	Total
1979	27 (84.5)	5 (15.5)	0 (0.0)	32
1980	44 (84.5)	7 (13.5)	1 (2.0)	52
1981	23 (85.2)	4 (14.8)	0 (0.0)	27
All years	94 (84.7)	16 (14.4)	1 (0.9)	111

that some larger family units may contain adopted young but the high amount of aggression observed between family groups seems to make this occurrence unlikely.

The yearly age ratio samples gathered in this study represent only approximately 10% of the Pacific Flyway lesser sandhill crane population. Efforts to census a larger number of cranes for proportions of juveniles ratios should continue. Tallying age ratios on the wintering grounds in California as the birds arrive in October may yield a greater sample size than could be obtained on the ECRD study area.

B. Sex Ratios

Among sandhill cranes I collected and those killed by hunters on the ECRD, a 60:40 (male:female) sex ratio was observed among 36 cranes where sex could be determined. This was not significantly different from an expected 50:50 ratio ($\chi^2 = 1.4$, df = 1, $p>0.05$). However, it does follow a trend observed in other studies of lesser sandhill cranes (Boeker et al. 1961, Guthery 1972, Johnson and Stewart 1973, Lewis 1974), where a slight preponderance of males was also noted. Stephen et al. (1966) found a ratio of 56.2:43.8 among 288 cranes was significantly different from an even sex ratio. This trend should be taken into consideration in computing population parameters for lesser sandhill cranes.

VII. HARASSMENT

The effects of disturbance from human-related sources, particularly aircraft, has only recently been investigated for large migratory birds (Davis and Wiseley 1974, Salter and Davis 1974, Dunnet 1977, Owens 1977, Kuehl 1979, Kushlan 1979). Reactions of sandhill cranes to human disturbance and aircraft activity during migration were poorly documented until recently (Kessel 1979*b*). Results of harassment studies have varied greatly among species and locations of the studies, indicating information at particular sites of interest is needed for species that may be adversely impacted by increased human disturbance.

A. Ground Observations

On the ECRD, 250 disturbances to staging crane flocks were noted from ground observation sites, covering all study periods from 1979-1981. Distribution of observations among the 7 disturbance sources were: eagles (106), eagles pursuing cranes (19), people approaching cranes in full view (22), people hidden from view (25), people hunting (29), small airplanes (including controlled overflights) (47), and helicopters (2).

Distances at which a potential source of disturbance flushes cranes would be expected to increase with the increasing threat

felt by cranes. Table 15 summarizes distances cranes flushed from the various disturbance sources. A Kruskal-Wallis analysis of variance revealed mean distances at which cranes flushed were not equal ($H = 51.89$, $df = 6$, $p<0.001$) among disturbance sources. Reactions of cranes to the 2 helicopters (Bell 206, large military helicopter) were at much greater distances than for all other sources, but sample size was too small for meaningful analysis. Cranes generally did not allow as close an approach from aerial disturbances (eagles, airplanes, helicopters) as from ground threats, but differences were not significant (Newman-Keuls Test, $p>0.05$), except in comparison to people hidden from view ($q = 4.05$, 3.90, $p<0.05$). This is to be expected as observers in the latter category purposefully crept closer to cranes than would have been possible if they had remained in the open.

Sample size for eagles pursuing cranes was also very low, but eagles intent on pursuing cranes appeared to gain closer access to flocks, probably due to increased speed of approach. Bald eagles flying over the study area flushed crane flocks in all observed cases where they approached the flock closer than 300 m. Pursuit of cranes occurred frequently on the ECRD. Bald eagles have been suspected of attacking sandhill cranes in Nebraska (Walkinshaw 1949, Lewis 1974), and observations of golden ealges (*Aquila chrysaetos*) attacking a sandhill crane (Johns 1977) and a whooping crane (Windingstad et al. 1981) have been recorded. On 10 May

Table 15. Approach distances (m) of disturbance sources to crane flocks at the time they flushed.

Disturbance source	Approach distance			
	Mean	SD	Range	n
Eagle:				
overflight	309	168	200-800	16
pursuing	133	76	20-200	3
Airplane	496	356	70-1600	25
Helicopter	2000	566	1600-2400	2
People:				
in the open	203	109	100-500	16
hidden	107	189	20-1000	25
hunting	138	187	30-800	16
All sources	254	340	20-2400	91

1980, I observed an adult bald eagle chase a flock of approximately 90 cranes and single out one individual. The eagle pursued this bird for almost 3.2 km, finally forcing it down to the ground and attacking it just before it landed.

Inspection of the crane carcass 1 h after the adult and a juvenile eagle had fed upon it showed the liver to be enlarged and covered with necrotic lesions. The condition of the liver was consistent with that caused by the bacteria *Streptococcus* spp., although definite determination of the organism involved could not be made on the preserved liver (R.A. Dieterich pers. comm.). The extent of the infection had likely stressed the individual as it was easily singled-out from other cranes by its slower, more labored flight after the eagle had chased the cranes for 1 km. Lewis (1974) isolated *Streptococcus* sp., *Herella* sp., and *Citrobacter* sp. from necrotic livers of sandhill cranes in the Central Flyway.

Other evidence of eagles predating cranes on the ECRD included a carcass mostly eaten by, and probably killed by an eagle on 4 September 1980. Repeated attacks by eagles on the taxidermy-mount crane decoys placed near the field camp in 1979 and 1980, also indicated they would readily attack sandhill cranes. These decoys were totally destroyed after up to 5 eagle attacks in each of the 2 years. Staging cranes were not flushed by marsh hawks (*Circus cyaneus*), gyrfalcons (*Falco rusticolus*) or other raptors or large birds other than eagles. Two eagles flying over cranes at about

the same time caused greater reactions than solitary eagles. Single brown bears were observed approaching crane flocks as close as 200 m before they flushed, on 19 September 1979 and 10 September 1981. This was approximately the distance a human could approach most crane flocks in the open. A flock of 11 cranes landed 500 m from a walking bear on 10 September 1981, and fed unconcerned as the bear moved off.

Few significant differences (Mann-Whitney U test, $p \leq 0.005$) occurred between spring and fall observations of flushing distances. However, cranes seemed to be more approachable in spring than in fall, particularly with regard to humans. Possibly this was a result of virtually no hunting pressure during the preceding winter season.

The directions at which cranes flushed from disturbance sources are summarized in Table 16. No significant differences occurred among disturbance types (Kruskal-Wallis $H = 9.35$, $df = 6$, $p > 0.05$), or between seasons ($p > 0.05$). The large angle of reaction indicated they generally flew directly (135-180°) away from a disturbance. Flushing directions were most variable for eagle overflights, and people hidden or hunting. Cranes pursued by eagles usually easily outdistanced them after flying 1 km. The wide variety of flushing directions in response to eagles may indicate cranes are not particularly threatened by eagles unless directly pursued. Under cover of shrubs or slough banks, people hidden from view and hunters could

Table 16. Reaction directions (degrees) of crane flocks in relation to direction of approach of disturbance sources.

Disturbance source	Reaction direction			
	Mean	SD	Range	n
Eagle:				
overflight	128	53	45-180	20
pursuing	167	30	80-180	10
Airplane	141	48	90-180	7
Helicopter	135	64	90-180	2
People:				
in the open	131	45	45-180	21
hidden	108	55	0-180	22
hunting	125	58	0-180	23
All sources	133	37	0-180	103

closely approach crane flocks. Often only a few birds became alarmed and flushed, while the majority of the flock could not assess where the disturbance originated and occasionally flew directly over the person. Cranes rarely flushed in less than a perpendicular direction (<90°) from major air threats such as pursuing eagles, airplanes, and helicopters. They eventually took a course perpendicular to the object to avoid being overtaken, if followed closely.

The distance cranes flew after being disturbed may also indicate different levels of harassment from the various disturbance sources (Table 17). Kruskal-Wallis analysis of variance on this parameter indicated mean distances were not equal for all sources ($H = 34.47$, $df = 6$, $p<0.001$). Subsequent Newman-Keuls tests showed distances flown by cranes after disturbance by pursuing eagles, airplanes, and hunters were significantly different ($q = 3.90$, 3.33, and 3.65, respectively; $p\leq0.05$) from eagle overflights. For all aerial disturbances, cranes occasionally circled around the disturbance and alighted in the same spot. This occurred more frequently (52% of all observations) with eagle overflights than for pursuing eagles (8%) or airplanes (21%). People approaching cranes in the open, as opposed to those hidden from view with resultant closer approach, did not cause different flight distances ($p>0.05$). Hunters tended to cause cranes to fly farther than from other human disturbance, but again, differences were not significant

Table 17. Distances (m) flown by cranes after disturbance.

Disturbance source	Distance flown			
	Mean	SD	Range	n
Eagle:				
overflight	890	1525	0-10,000	106
pursuing	2500	2643	0-10,000	12
Airplane	1852	2425	0-10,000	23
Helicopter	800	0	800-800	2
People				
in the open	1519	1089	200-3200	21
hidden	1325	1310	40-4800	16
hunting	2005	1990	50-6400	29
All sources	1338	1726	0-10,000	200

($p>0.05$). Instances of crane flocks departing the ECRD immediately after disturbance were noted for all eagle and people categories and could have occurred after aircraft disturbances, but sample sizes in these categories were low. If weather conditions for migration were favorable, cranes disturbed during early morning hours often left the ECRD, but usually not more than 1-2 h earlier than flocks not disturbed. As with approach distances, flight distances did not vary significantly between seasons (Mann-Whitney U test, $p \leq 0.05$).

An increasing amount of time spent in the air following a disturbance would mean less time for feeding, and could adversely impact staging cranes. Flight time was highly correlated with distance cranes flew (Spearman's Rank Correlation, $r_s = 0.60$, $n = 60$, $p \leq 0.001$; Zar 1974), as expected, because farther distances required longer flight times. Cranes that spent more time in the air than expected by the distance they travelled could indicate a higher amount of disturbance. Using a mean figure of 50 km/h for crane flight speed (Cottam et al. 1942, Walkinshaw 1949, Kessel 1979*b*), I calculated expected flight times based on distance flown for each disturbance category. Comparisons between expected and observed flight times showed significant differences only for eagle overflights ($S^2 = 25.4$, $df = 2$, $p \leq 0.001$). Cranes may remain in the air longer when eagles are nearby in order to ascertain predatory intentions of these raptors. For all disturbance sources, time

spent in the air averaged less than 5 min. On few occasions were cranes in the air for more than 15 min, usually after multiple encounters with hunters or during long distnnce flights across the study area.

The distance at which brant (*Branta bernicla*) flocks flushed from human disturbances increased with increasing flock size in Britain (Owens 1977). Spearman's Rank Correlations relating flock sizes of cranes on the ECRD with disturbance parameters showed low correlations (r_s <0.10), except for approach distance (r_s = 0.343, n = 60, p<0.01). Larger flocks usually flushed at greater distances than did small flocks, especially for people categories (r_s > 0.50, n = 16, $p \leq 0.05$).

The amount of time cranes had been at a site was not significantly correlated with reactions to disturbance ($-0.20 < r_s < 0.20$, n = 60, p>0.05). Correlations were usually positive with flight times and distances, however, indicating a readiness on the part of cranes to fly after they had remained at a site for a long period of time. Owens (1977) noted similar behavior with brant, where 'normal' flights to new feeding areas were often initiated sooner due to a disturbance, but would have happened eventually had a disturbance not occurred.

Although based on only 2 observations, the very long approach distances and the strong escape response exhibited, suggested cranes were most disturbed by helicopter overflights. Kessel

(1979*b*) also noted helicopters caused cranes to react at greater distances than did small airplanes. Results from studies of other birds were variable; Kushlan (1979) noted equal or less disturbance of nesting egrets and herons from helicopters compared to fixed-wing aircraft, but work with flocks of geese indicated stronger reactions occurred from helicopters than airplanes (Davis and Wiseley 1974, Owens 1977). In the last two studies, both brant and snow geese became habituated to aircraft, showing less reaction after repeated overflights. Snow geese, however, reacted more strongly if overflights occurred frequently over short intervals. Sandhill cranes in this study seemed to exhibit some habituation to fixed-wing aircraft overflights which probably occur commonly over breeding and wintering areas, but less so to helicopters, with which they probably have fewer encounters.

Airplanes appeared to be slightly less disturbing to cranes than helicopters, but pursuing eagles and hunters were also major threats. People approaching cranes, and for most measures, eagle overflights, caused the least amount of disturbance as cranes often landed short distances away or even in the same spot in the case of the latter source.

Whether stress caused by existing disturbances or experimental airplane overflights was particularly detrimental to cranes could not be measured in this study. Time budget information and fat deposition data are needed to better assess affects of disturbance

to cranes staging on the ECRD. Small amounts of disturbance to snow geese staging on the North Slope of Alaska and the Yukon, led to possible reductions of 20.4% in energy storage to juveniles (Davis and Wiseley 1974). In years when almost all flocks of cranes passing through the ECRD need to stage for several days or possibly weeks, stress caused by additional human-related disturbance may be detrimental to the physiological needs of staging cranes. The unusual situation on the ECRD, of high bald eagle and sandhill crane populations together on the same area in fall, results in a fairly high amount of natural harassment. Additional souces of disturbance under these conditions could be especially detrimental to staging cranes.

B. Airborne Observations

Response behaviors of cranes to experimental airplane overflights are given in Table 18. The predominance of escape behaviors indicated cranes were frightened by the plane on most occasions, but no panic behavior was observed. Strong escape responses were often given initially until the plane had passed over, then cranes quickly resumed normal flight speeds. Passes directly over cranes generally initiated stronger responses than if the flock were off to one side. On 14 September 1981, a Cessna 185 was flown over a feeding flock of 500 cranes at 60 m, but only

Table 18. Frequency of response behaviors of sandhill crane flocks to experimental aircraft overflights.

Aircraft type	Response					
	None	Alert	Mild escape	Strong escape	Panic	Total
Cessna 185	4	7	10	16	0	37
Beaver	0	1	2	1	0	4
Total	4	8	12	17	0	41

approximately 50 birds directly below the plane flushed and soon alighted. Cases in which the cranes did not fly (none, alert) may be underrepresented because cranes were often difficult to see against the browning sedges and grasses of the Wet Meadow habitat. Several times, cranes were first noticed only when they flushed.

A tendency existed for cranes to react more strongly to planes flying at lower altitudes, but differences were not significant between plane altitudes of < 60 m and ≥ 60 m ($\chi^2 = 0.26$, df = 1, $p>0.05$). Ferguson et al. (1979) found it necessary to fly over cranes with a Cessna 180 at 30-45 m to flush them for censuses. Cranes on the ECRD flushed only 68% of the time at these heights with a Cessna 185. Other factors, including previous habituation of groups of cranes to planes and weather factors, probably influenced crane reactions. Cranes were flushed by the plane less often when weather was bad (moderate precipitation and/or winds > 20 km/h) than when fair weather (no precipitation, light winds) prevailed ($\chi^2 = 4.15$, df = 1, $p>0.05$). Crane flock size, as well as the position of the sun to the aircraft, or aircraft activity such as circling and multiple passes did not seem to alter crane responses significantly. Aircraft loudness may affect crane reactions, however. Planes taking off from sloughs flushed flocks of feeding cranes up to 0.80 km away. Decibel levels of Beaver aircraft were probably higher than those of the Cessnas. Cranes were flushed by the Beaver on 3 of 4 overflights at approximately 60 m, but flushed 4 times out of 8 at that altitude with a 185.

Flying cranes were encountered on 4 occasions while an observer was in the plane. A flock of 20 cranes reversed their direction while still 500 m from a 185 approaching from in front of them. They circled around the plane at increased speed, then resumed their original direction. Flocks encountered from behind or below allowed approaches of 200-250 m before increasing speed or veering to one side to avoid the plane. Kessel (1979*b*) also noted cranes reacted at greater distances to planes approaching in front of migrating flocks.

Present harassment levels of cranes by aircraft on the ECRD appear minimal. One instance of direct harassment by a Beaver aircraft was observed in September 1979, when the plane was maneuvered to drive cranes toward waiting hunters. The cranes eventually flew to Salt Grass Meadow habitat after 5 min of harassment. An increase in air traffic could, however, lead to harassment problems, especially in years of lengthy staging by cranes.

No aircraft ceiling levels currently exist over the Copper River Delta (R. Burraychak pers. comm.). Small planes remaining at least 100 m or higher above ground level except during approaches to landing sites should minimize most disturbance to cranes. Larger planes and helicopters may need to remain at higher altitudes. To minimize harassment to migrating cranes and eliminate the chance of air strikes, pilots should attempt to remain 300 m from flying crane flocks.

SUMMARY AND CONCLUSIONS

Migration and staging of sandhill cranes on the eastern Copper River Delta were studied in spring of 1979 and 1980, and fall of 1979, 1980, and 1981. Yearly, an estimated 20,000-22,000 sandhill cranes pass through the ECRD, at least during fall migration. Lower numbers are observed in spring when migration progresses at a more rapid pace, with night migrations and movements beyond the sight or hearing of observers occurring frequently. Sandhill cranes first arrived on the study area in mid- to late April, and continued through mid-May, with peak migration during the last days of April and the first week of May. Fall migrants arrived in mid- to late August and continued through mid-October. Peaks of migration occurred in mid- to late September. In fall 1979, almost all flocks of cranes reaching the ECRD staged for 1-10 days. Flocks of cranes frequently overflew the ECRD in fall 1980 and 1981, though some staging still occurred. Foul weather periods lengthened staging times of many crane flocks. Wind speed and direction, precipitation, cloud cover, and other weather variables all probably play a role in determining volume of migration for these fair-weather migrants.

Other migrant waterbirds on the ECRD belong to Pacific Flyway stocks, but it was not definitely known whether sandhill cranes staging on the ECRD migrated within this flyway. Capturing sandhill

cranes on the ECRD was impractical, so attempts were made to rocket-net cranes wintering in California. Forty-three lesser sandhill cranes were captured and color-marked with red leg bands and neck collars at Merced NWR, California, in February and March 1980. Up to 6 of these marked cranes were subsequently resighted on the ECRD in spring and fall 1980 and fall 1981. One was resighted during fall in southeastern Alaska, and 7 in Oregon during spring. None of the over 3000 sandhill cranes marked at Central Flyway locations have as yet been sighted in the Pacific Flyway. It therefore appears that the 20,000-25,000 lesser sandhill cranes wintering in central California migrate through Pacific Flyway states and provinces, with the bulk of the population staging on the ECRD in fall. Breeding grounds of this population are as yet undetermined, but migration observations point toward lowland areas of Cook Inlet and Bristol Bay as likely sites. Color-marking of juveniles on suspected breeding grounds with resightings on the more "peopled" wintering areas would easily document breeding locations.

At the present time, consumptive use of the Pacific Flyway population of lesser sandhills is restricted to Alaska where sport hunting and subsistence harvests occur. Kramer et al. (1981) presented data on the sport harvest of cranes in Alaska as obtained from state and federal mail surveys. The past ten years' average was estimated at 229 birds (range = 90-490) for Pacific Flyway stocks. Subsistence harvest of adult, young, and eggs of sandhill

cranes on the Yukon-Kuskokwim Delta has been estimated at 1033 birds by Klein (1966), and 1477 birds and eggs by Copp and Smith (1981). Subsistence harvest of Pacific Flyway lesser sandhills is believed to be negligible (Kramer et al. 1981), although some annual harvest may occur near villages in the Bristol Bay area. Information on age structure of the population, age and density related breeding success, and accurate population estimates are needed to assess the impact of hunting and maintenance of harvest levels on Pacific Flyway lesser sandhill cranes.

Body measurements and measurements of track impressions revealed ECRD cranes had, overall, slightly larger measurements than typical lesser sandhill cranes. A few birds could be classified as the intermediate-sized Canadian sandhill crane. Classification of the 3 most widespread subspecies of sandhill cranes has been debated (Stephen 1967, Tacha 1981) due to continuous clinal trends from the larger greater sandhill cranes to the smaller lessers, and poor definition of breeding areas of Canadian sandhill cranes. Populations utilizing specific breeding, staging, or wintering sites has been suggested for use as the basis for sandhill crane management (Stephen 1967, Tacha 1981). The distinct use areas of Pacific Flyway lesser sandhills lend themsleves to management at such a population level.

Food habits of sandhill cranes staging on the ECRD were determined by analysis of gizzard and gullet contents of collected and hunter-bagged birds. Cranes fed predominantly (90-95% by volume) on

arrow-grass (*Triglochin palustris*), extracting the fleshy bulbs of the plant. Nutritional analysis of *T. palustris* bulbs showed they were high in carbohydrates (35.6%) and protein (14.8%) on a dry-weight basis. Thomas and Prevett (1980) concluded the bulbs were a high-quality pre-migratory food for geese at James Bay. The high carbohydrate levels provide energy for protein synthesis and fat deposition, while protein levels in the bulbs provide the necessary basics for strengthening of flight muscles. Additional essential amino acids are probably obtained from animal prey taken by cranes. Adult and larval craneflies and snails were common prey remains in crane food samples. During peak population levels of tundra voles, as in fall 1981, cranes readily captured and consumed these rodents.

Observations of local movements of staging cranes were mapped, and high use areas on the ECRD determined. Traditional use of open meadows for feeding in the Russian River Slough area appears to be declining, as shrub invasion, following uplift from the 1964 earthquake, continues. Increased use of open areas near the Spruce Islands, and increased competition for food with geese appears likely in the future. Comparison of systematic vegetation plots across the Wet Meadow and plots taken at crane feeding sites indicated cranes preferred moist or fairly dry sites near the Wet Meadow-Medium Shrub habitat interface. Plant species found more often in feeding plots than expected based on the systematic vegetation plots included *Carex ramenskii, Poa eminens, Calamagrostis* spp.,

and *Agrostis* spp., with a moss cover of *Rhytidiadelphus squarrosus*, *Aulacomnium palustre*, *Mnium pseudopunctatum*, and *Sphagnum squarrosum*. Feeding habitat availability in the Wet Meadow type, as measured in fall 1980, was estimated at about 20% of this habitat, or 10 km^2 in areas now used by cranes.

Cranes utilized roost sites in all 4 major habitat types on the ECRD. Habitat selection was not affected significantly by tidal stage or weather, although cranes were occasionally grounded in Wet Meadow feeding areas by severe storms. Cranes tended to avoid exposed Intertidal Mudflat and Salt Grass Meadow roost sites during severe weather. Most cranes arrived at roost sites within 1 h of sunset and departed just prior to sunrise.

Consistent crane use of the ECRD, after bypassing the marshes of the WCRD in fall, may be due to several factors: 1. traditional use of feeding sites on the ECRD, 2. differences in substrate types, plant species, and moisture regimes, 3. more frequent development of air thermals, 4. geographic setting on the distal end of the migration direction. Whatever the cause, however, the ECRD has the bulk of crane use of all Copper River and Bering River coastal wetlands. Shrub expansion in the Wet Meadow is the major threat to crane habitat at the present time. Maintenance of openings by mechanical or chemical methods would be expensive, impractical, and probably undesirable in such a wilderness setting as the ECRD. Adaptation to feeding in the Salt Grass Meadow habitat or possibly

on WCRD or Bering River Delta sites will hopefully occur in the future, should shrub expansion result in exclusion of cranes in of Wet Meadow habitat on the ECRD.

Development of offshore oil reserves in the Gulf of Alaska and oil fields near Katalla, 25 km east of the ECRD, could increase the possibility of pollution of nearby marine waters. Oil pollution could have deleterious effects on Salt Grass Meadow communities should a spill occur near the ECRD. Monitoring of crane use of habitat types on the ECRD should continue in view of the rapid successional changes occurring there, and potentially harmful resource developments planned in the immediate area.

Proportions of juvenile and adult cranes, as determined by head coloration, were noted as opportunity permitted to assess productivity of this population. Observed age proportions were 7% in fall 1979 and 1980, but were approximately 11% in 1981. Mean proportions of 11% juveniles have been noted among Central Flyway sandhill cranes (Buller 1976). Pacific Flyway lesser sandhills may have had poor production on breeding areas in 1979 and 1980, but the 11% level of juveniles in 1981 shows they can, at times, equal production levels of Central flyway birds. Continued monitoring of age composition in September and October on the ECRD, or as cranes arrive on the wintering grounds in California in October, would better document productivity of this population.

Reactions of staging cranes to disturbance were noted from ground locations and during experimental overflights in small planes. Helicopters initiated flushing reactions from cranes at the greatest distance (2000 m), followed by small planes, people, and bald eagles. Cranes tended to fly farther after disturbance by planes and hunters than for people (other than hunters) and bald eagles. Habituation to airplanes seems to have occurred among most cranes as several flocks showed little reaction to planes as low as 30 m in altitude. Cranes were never observed to panic in efforts to escape from planes, although strong escape responses were noted. Planes remaining 100 m or higher should cause minimal disturbance and loss of feeding time. Helicopters and large planes remaining 300 m or higher should not cause undue disturbance of staging cranes.

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Appendix I. List of birds observed on the eastern Copper River Delta and the status of each species. Observation periods included: 27 April - 22 October 1979, 19 April - 20 May and 18 August - 20 October 1980, and 27 August - 28 September 1981. Status abbreviations and terminology follow Kessel and Gibson (1978): A=abundant, C=common, U=uncommon, and R=rare. Further discussion of the status and biology of birds on the ECRD is presented in Mickelson et al. (1980).

Species	Status	Species	Status
common loon	U breeder	American wigeon	C migrant C breeder
arctic loon	U migrant	northern shoveler	C migrant U breeder
red-throated loon	U breeder	canvasback	R migrant
red-necked grebe	R migrant	ring-necked duck	R breeder
horned grebe	R migrant	greater scaup	C migrant U breeder
double-crested cormorant	U visitant	common goldeneye	U migrant U breeder
great blue heron	R visitant	Barrow's goldeneye	U migrant
whistling swan	C migrant	oldsquaw	U migrant
trumpeter swan	C breeder	white-winged scoter	C migrant
Canada goose	A migrant C breeder	surf scoter	C migrant
brant	U migrant	black scoter	C migrant
white-fronted goose	C migrant	bufflehead	U migrant
snow goose	C migrant	eider sp.	R visitant
emperor goose	R visitant	common merganser	U breeder
mallard	A migrant C breeder	red-breasted merganser	C breeder
pintail	A migrant C breeder	goshawk	U migrant
gadwall	U migrant U breeder	sharp-shinned hawk	U migrant
blue-winged teal	R visitant	red-tailed hawk	U migrant
green-winged teal	A migrant C breeder	rough-legged hawk	U migrant

Appendix I. (cont.)

bald eagle	C resident	least sandpiper	C migrant A breeder
marsh hawk	C migrant U breeder	dunlin	A migrant R breeder
osprey	U migrant	rock sandpiper	R migrant
gyrfalcon	U migrant	red knot	U migrant
peregrine falcon	U migrant	short-billed dowitcher	A migrant C breeder
merlin	C migrant	long-billed dowitcher	C migrant
American kestrel	U migrant	stilt sandpiper	R visitant
willow ptarmigan	U resident	semipalmated sandpiper	U migrant
sandhill crane	A migrant	western sandpiper	A migrant
killdeer	U visitant	marbled godwit	R migrant
American golden plover	C migrant	Hudsonian godwit	U migrant
black-bellied plover	C migrant	sanderling	U migrant
surfbird	U migrant	red phalarope	R migrant
ruddy turnstone	U migrant	northern phalarope	A migrant C breeder
black turnstone	U migrant	parasitic jaeger	C breeder
common snipe	C migrant C breeder	herring gull	R resident
whimbrel	C migrant	glaucous-winged gull	A resident
bristle-thighed curlew	R migrant	mew gull	C migrant C breeder
upland sandpiper	R visitant	Bonaparte's gull	C migrant
spotted sandpiper	U breeder	black-legged kittiwake	U migrant
wandering tattler	U migrant	arctic tern	A breeder
greater yellowlegs	C migrant	Aleutian tern	A breeder
lesser yellowlegs	U migrant	marbled murrelet	R visitant
solitary sandpiper	U migrant		
sharp-tailed sandpiper	R migrant		
pectoral sandpiper	A migrant		

Appendix I. (cont.)

mourning dove	R visitant	red-breasted nuthatch	U resident
great horned owl	C resident	brown creeper	C resident
short-eared owl	C migrant C breeder	dipper	U resident
hawk owl	U breeder	winter wren	U resident
boreal owl	R visitant	American robin	C migrant C breeder
rufous hummingbird	U migrant	varied thrush	C migrant C breeder
belted kingfisher	U resident	hermit thrush	C migrant C breeder
common flicker	U migrant	Swainson's thrush	U migrant
hairy woodpecker	U resident	ruby-crowned kinglet	C resident
downy woodpecker	U resident	golden-crowned kinglet	C resident
yellow-bellied sapsucker	R resident	yellow wagtail	R visitant
Say's phoebe	R visitant	water pipit	A migrant
alder flycatcher	U breeder	northern shrike	U migrant
olive-sided flycatcher	R visitant	starling	R visitant
horned lark	U migrant	orange-crowned warbler	A migrant C breeder
tree swallow	C migrant C breeder	yellow warbler	C migrant C breeder
bank swallow	C migrant U breeder	yellow-rumped warbler	C migrant C breeder
barn swallow	U breeder	Townsend's warbler	C breeder
cliff swallow	R migrant	blackpoll warbler	U migrant
Steller's jay	U resident	Wilson's warbler	C migrant C breeder
black-billed magpie	C resident	rusty blackbird	U migrant
common raven	C resident		
northwestern crow	R visitant		
black-capped chickadee	U resident		
chestnut-backed chickadee	C resident		

Appendix I. (cont.)

brown-headed cowbird	R visitant	white-crowned sparrow	C migrant
pine grosbeak	R resident	golden-crowned sparrow	C migrant
common redpoll	C resident	fox sparrow	C migrant
pine siskin	U resident		U breeder
savannah sparrow	A migrant	Lincoln's sparrow	C breeder
	A breeder	song sparrow	U breeder
dark-eyed junco	U migrant	Lapland longspur	A migrant
tree sparrow	U migrant	snow bunting	U migrant

Appendix II. List of mammals observed on the eastern Copper River Delta and adjacent coniferous forest and alpine habitats from 27 April - 22 October 1979, 19 April - 20 May and 18 August - 20 October 1980, and 27 August - 28 September 1981.

Common name	Scientific name
masked shrew	*Sorex cinereus*
little brown bat	*Myotis lucifugus*
black bear	*Ursus americanus*
brown bear	*Ursus arctos*
least weasel	*Mustela rixosa*
shorttail weasel	*Mustela erminea*
mink	*Mustela vison*
river otter	*Lutra canadensis*
wolverine	*Gulo gulo*
coyote	*Canis latrans*
wolf	*Canis lupus*
harbor seal	*Phoca vitulina*
hoary marmot	*Marmota caligata*
beaver	*Castor canadensis*
tundra red-backed vole	*Clethrionomys rutilis*
tundra vole	*Microtus oeconomus*
muskrat	*Ondatra zibethica*
porcupine	*Erethizon dorsatum*
moose	*Alces alces*
mountain goat	*Oreamnos americanus*

Appendix III. Cover and frequency of plants found on 129 1-m^2 vegetation plots in Wet Meadow habitat on the eastern Copper River Delta, Alaska.

Species	Mean percent cover	% Frequency of occurrence
Aulocomnium palustre	17.7	50.4
Drepanocladus uncinatus	11.5	34.9
Rhytidiadelphus squarrosus	10.7	27.9
Mnium pseudopunctatum	8.0	45.7
Helodium blandowii	5.4	33.3
Psilopilum laevigatum and *Dicranella* sp.	5.2	12.4
Polytrichum commune	4.4	25.6
Myrica gale	4.2	24.8
Carex lyngbyaei	3.8	51.2
Alnus sinuata	3.4	31.0
[a]Upright *Salix* spp.	3.3	32.5
Potentilla egedii	2.6	75.2
Equisetum arvense and *Equisetum fluviatile*	1.9	55.0
[b]Dwarf *Salix* spp.	1.8	33.3
Agrostis alaskana and *Agrostis geminata*	1.0	44.2
Poa eminens	0.86	48.8
Juncus alpinus	0.81	27.9
Sphagnum squarrosum	0.70	8.5

Appendix III. (cont.)

Epilobium palustre and *E. hornemannii*	0.53	63.6
Parnassia palustris	0.51	50.4
Potentilla palustris	0.46	10.1
Deschampsia beringensis	0.46	22.5
Epilobium angustifolium	0.45	3.1
Chrysanthemum arcticum	0.44	26.4
Eleocharis kamtschatica	0.43	12.4
Calamagrostis deschampsioides	0.41	21.7
Calamagrostis canadensis	0.41	32.6
Peltigera sp.	0.35	17.8
Primula egaliksensis	0.30	9.3
Rhinanthus minor	0.29	46.5
Populus trichocarpa	0.28	3.9
Picea sitchensis	0.21	6.2
Triglochin maritimum	0.21	17.1
Galium trifidum	0.21	29.5
[c]*Stellaria* spp.	0.20	32.5
Lathyrus palustris	0.19	5.4
Eleocharis palustris	0.19	2.3
Carex mackenziei	0.19	5.4
Carex pluriflora	0.19	2.3
Eriophorum scheuchzeri	0.18	16.3

Appendix III. (cont.)

Rumex fenestratus	0.17	8.5
Pyrola asarifolia	0.15	1.5
Spiranthes romanzoffiana	0.14	22.5
Hedysarum alpinum	0.12	1.6
Carex aquatilis	0.12	4.6
Ranunculus cymbalaria	0.11	13.9
Epilobium adenocaulon	0.10	10.9
Deschampsia caespitosa	0.09	5.4
Agrostis exarata	0.08	7.0
Plantago maritima	0.08	5.4
Viola epiesila	0.08	3.8
Lycopodium sp.	0.08	1.5
Hippuris tetraphylla	0.07	2.3
Cicuta douglasii and *C. mackenzieana*	0.06	5.4
Euphrasia mollis	0.06	10.8
Drosera rotundifolia	0.05	1.6
Mushroom spp.	0.04	7.0
Triglochin palustris	0.04	7.8
Lomatogonium rotatum	0.03	6.2
Pedicularis verticillata	0.03	2.3
Juncus arcticus	0.02	3.1
Juncus castaneus	0.02	1.5

Appendix III. (cont.)

Festuca rubra	0.02	5.4
Festuca altaica	0.02	3.1
Eriophorum russeolum	0.01	1.5
Carex kelloggii	0.01	0.8
Carex laeviculmis	0.01	2.3
Hierochloe odorata	0.01	2.3
Iris setosa	0.01	0.8
Juncus falcata	<0.01	0.8
Manyanthes trifoliata	<0.01	0.08
Platanthera dilatata	<0.01	0.08
Ranunculus hyperboreus	<0.01	0.08
Athyrium felix-femina	<0.01	0.08
Hammarbya paludosa	<0.01	0.08

[a]This category consists of willow species of upright growth form. Some of the species present on the study area were identified and include: *Salix alaxensis*, *S. barclayi*, *S. commutata*, *S. scouleriana*, and *S. sitchensis*.

[b]This category consists of willow species of mat-forming growth form. Some of the species identified on the study area include: *S. arctica*, and *S. ovalifolia*.

[c]This category consists of species of *Stellaria* found on the study area. Some of the species identified include: *S. calycantha*, *S. humifusa*, and *S. longifolia*.

Appendix IV. Cover and frequency of plants on 24 1-m^2 vegetation plots taken in Salt Grass Meadow habitat on the eastern Copper River Delta, Alaska.

Species	Mean percent cover	% Frequency of occurrence
Psilopilum laevigatum and *Dicranella* sp.	39.6	20.8
Carex ramenskii	18.2	16.7
Plantago maritima	11.7	50.0
Potentilla egedii	8.6	54.2
Puccinella spp.	4.2	75.0
Deschampsia caespitosa	3.9	37.5
Carex lyngbyaei	2.7	20.8
Equisetum arvense	1.5	16.7
Juncus arcticus	1.5	37.5
Myrica gale	1.4	4.2
Alnus sinuata	1.3	4.2
Juncus bufonius	1.0	8.3
Dwarf *Salix* spp.	0.8	8.3
Ranunculus cymbalaria	0.7	16.7
Triglochin palustris	0.7	8.3
Parnassia palustris	0.4	16.7
Epilobium palustre	0.3	12.5
Hordeum brachyantherum	0.2	4.2
Juncus alpinus	0.2	12.5

Appendix IV. (cont.)

Chrysanthemum arcticum	0.2	4.2
Rhinanthus minor	0.2	8.3
Polygonum fowleri	0.2	4.2
Polytrichum commune	0.1	4.2
Agrostis exarata	0.1	4.2
Agrostis alaskana and *A. geminata*	0.02	4.2

Appendix V. Plants identified on the eastern Copper River Delta but not found in systematic vegetation plots in Wet Meadow or Salt Grass Meadow habitat. Species occurring only on gravel bars along major sloughs or on sand dunes (*a*), in an acidic bog near Mirror Slough (*b*), or in coniferous uplands (*c*) are noted

Achillea borealis	*Elymus arenarius*
Alopecurus aequalis	*Empetrum nigrum*
[b]*Andormeda polifolia*	[a]*Epilobium latifolia*
[c]*Aquilegia formosa*	*Eriophorum angustifolium*
Arctophila fulva	*Fritillaria camschatcensis*
Aruncus sylvester	[b]*Gentiana douglasiana*
[c]*Boschniakia rossica*	[c]*Geranium erianthum*
[c]*Botrychium lunaria*	*Geum calthafolia*
Callitriche verna	[a]*Geum macrophyllum*
Caltha palustris	[a]*Glehnia littoralis*
Cardamine pratensis	[c]*Gymnocarpium dryopterus*
Carex rhynchophysa	*Heuchera glabra*
Carex rostrata	*Hippuris vulgaris*
Carex sitchensis	[a]*Honckenya peploides*
Cassiope stellariana	*Isoetes truncata*
Castilleja chrymactis	[c]*Lysichiton americanum*
Corallorrhiza trifida	[c]*Maianthemum dilatatum*
Cornus canadensis	*Malaxis monophylla*
[b]*Dodecatheon jeffreyi*	[c]*Menziesia ferruginea*
[c]*Dryopterus dilatata*	[c]*Mimulus guttatus*
[c]*Echinopanax horridum*	*Moehringia laterifolia*

Appendix V. (cont.)

[c]*Moneses uniflora*	*Sagina intermedia*
Myriophyllum spicatum	[c]*Sambucus callicarpa*
[b]*Nuphar polysepalum*	*Sanguisorba stipulata*
Oxycoccus microcarpus	*Saxifraga punctata*
Phyllodoce aleutica	*Scirpus validus*
Pinguicula vulgaris	*Sedum rosea*
Polemonium acutiflorum	[a]*Senecio pseudo-arnica*
[a]*Polygonum viviparum*	*Solidago lepida*
Potentilla villosa	*Sparganium angustifolium*
Potamogeton natans	*Spiraea beauverdiana*
Potamogeton pectinatus	*Streptopus amplexifolius*
Potamogeton perfoliatus	[c]*Tiarella trifoliata*
Prenanthes alata	*Trientalis europaea*
Rhododendron camtschaticum	[c]*Tsuga heterophylla*
[c]*Ribes laxiflorum*	[c]*Vaccinium ovalifolium*
[a]*Rorrippa islandica*	*Vaccinium uliginosum*
[c]*Rubus pedatus*	[c]*Veratrum viride*
Rubus spectabilis	[c]*Viburnum edule*